TROPHIC DYNAMICS AND STOCK CHARACTERISTICS OF SNOW CRABS, *CHIONOECETES OPILIO*, IN THE ALASKAN ARCTIC

By

Lauren Mallory Divine, B.S., M.S.

A Dissertation Submitted in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

in

Marine Biology

University of Alaska Fairbanks

August 2016

APPROVED:

Katrin Iken, Committee Chair
Bodil A. Bluhm, Committee Member
James R. Lovvorn, Committee Member
Gordon H. Kruse, Committee Member
Franz J. Mueter, Committee Member
Sarah M. Hardy, Department Chair, *Department of Marine Biology*
Bradley Moran, Dean, *School of Fisheries and Ocean Sciences*
John C. Eichelberger, Dean, *Graduate School*

ABSTRACT

Arctic waters off the coast of Alaska have become increasingly open to human activities via dramatic climatic changes, such as reduced sea ice thickness and extent, warming ocean temperatures, and increased freshwater input. This research advances knowledge of snow crab trophic dynamics and stock characteristics in Arctic waters off the Alaska coast. Here, I provided baseline information regarding snow crab position in Beaufort Sea benthic food webs, its specific dietary habits in the Chukchi and Beaufort seas, and expanded upon previously limited life-history and population dynamic data in the Chukchi and Beaufort seas.

I first detailed benthic food webs on the Alaskan Beaufort Sea shelf and snow crab trophic positions within these food webs using stable $\delta^{13}C$ and $\delta^{15}N$ isotope analysis. Water column and sediment particulate organic matter (POM) were used as primary food web end members. Isotopic niche space ($\delta^{13}C - \delta^{15}N$) occupied by benthic taxa provided measures of community-wide trophic redundancy and separation. Water column and sediment POM $\delta^{13}C$ values generally reflected terrestrial POM inputs in the eastern and central shallow (14-90 m) Beaufort regions, but were indicative of persistent marine influence in the western and central deep (100-220 m) regions. Food web structure, as reflected by consumer trophic levels (TLs), trophic redundancy, and trophic niche space, supported the POM findings. In the eastern and central shallow regions, consumers occupied mainly lower TL (TL= 1-3), whereas consumers in the western regions occupied intermediate and higher TL (TL= 3-4). Overall trophic redundancy and niche space occupied by food webs in these four regions, however, was similar. The central deep Beaufort food web was unique in all metrics evaluated, and the comparatively largest isotopic niche space, with high trophic niche separation but low trophic redundancy, suggests that this region may be most vulnerable to perturbations. Snow crabs occupied food webs in the central deep and

western shallow and deep Beaufort regions, where they maintained a consistent TL of 4.0 across regions.

I then investigated snow crab dietary habits across the Chukchi, and the Alaskan and Canadian Beaufort seas in the size range of 40 to 130 mm CW using stomach contents and stable isotope analyses. Snow crabs consumed four main prey taxa: polychaetes, decapod crustaceans (crabs, amphipods), echinoderms (mainly ophiuroids), and mollusks (bivalves, gastropods). Crab diets in the southern and northern Chukchi Sea regions were similar to those in the western Beaufort Sea in that bivalve, amphipod, and crustacean consumption was highest. The Canadian Beaufort region was most unique in prey composition and in stable isotope values. Cannibalism on snow crabs was higher in the Chukchi Sea regions relative to the Beaufort Sea regions, suggesting that cannibalism may have an impact on recruitment in the Chukchi Sea via reduction of cohort strength after settlement to the benthos, as known from the Canadian Atlantic. Based on a comparison with southern Chukchi Sea macrofauna data, these results document the non-selective, omnivorous role of snow crabs across the entire Pacific Arctic, as well as providing first evidence for cannibalism in the Chukchi Sea.

Finally, I generated new estimates of stock biomass, abundance, and maximum sustainable yield, length-weight relationships, size-at-maturity, and fecundity of snow crab in the Alaskan Arctic. Although snow crabs were more abundant in the Chukchi Sea, no crabs larger than the minimum marketable size (> 100 mm carapace width, based on Bering Sea metric) occurred in this region. Harvestable biomass of snow crabs only occurred in the Beaufort Sea, but was considerably lower than previous estimates in the Arctic FMP. Length-weight relationships were generally similar for male and female snow crabs between the Chukchi and Beaufort seas. Size-at-maturity and female fecundity in the Chukchi Sea were similar to snow crabs occurring in other geographic regions; low sample sizes in the Beaufort prevented size-at-maturity and fecundity analysis. Together these results contribute new

understanding of Arctic snow crab population dynamics by utilizing a rich dataset obtained recently from the Chukchi and Beaufort regions.

TABLE OF CONTENTS

LIST OF FIGURES

Page

Chapter 1

Chapter 2

Chapter 3

LIST OF TABLES

Page

Chapter 1

Chapter 2

Chapter 3

INTRODUCTION

The Arctic Ocean is experiencing dramatic changes, including reduced sea ice extent and thickness, rising ocean temperatures, and increased freshwater input. Changes are especially prominent in the marginal seas of Alaska, including the northern Bering, Chukchi, and Beaufort seas (Steele et al. 2008, 2010, Grebmeier 2012). The northern Bering and Chukchi seas are highly productive shelves where intense primary production in the water column is tightly coupled to benthic secondary production because only a comparatively small fraction of phytoplankton production is consumed by zooplankton communities (Grebmeier 2012). The Beaufort shelf, although less productive than the Chukchi shelf, is more productive relative to the adjacent Arctic Basin (Hill and Cota 2005) and hosts patchy but fairly rich benthic communities with respect to diversity, abundance, and biomass (Ravelo et al. 2015). These benthic communities comprise important food sources for higher trophic level fish, seabirds, and marine mammals (Moore 2008, Lovvorn et al. 2009). However, predicted future changes in the timing and intensity of phytoplankton blooms, as are predicted in future warming scenarios across the Arctic, may reduce the degree of benthic-pelagic coupling and increasingly shunt primary production to a pelagic-dominated food web with unpredictable consequences in both the pelagic and benthic realms (Wassmann 2011). Simultaneously, the Alaskan Arctic is becoming progressively open to human activities such as oil and gas exploration and development and marine shipping traffic (Smith and Stephenson 2013). The collective effects of natural climate variability and anthropogenic impacts on the underlying marine ecosystems (e.g., species range shifts, expansions and contractions, community composition, and carbon cycling) are of great concern to a wide range of stakeholders including local communities, scientists, resource managers, and local, state, tribal, and federal governments.

Biological changes have already been documented across the Bering, Chukchi, and Beaufort seas (e.g., Mueter and Litzow 2008, Lovvorn et al. 2009, Rand and Logerwell 2011, Grebmeier 2012, Renaud et al. 2015). A notable example includes the northward contraction of the center of distribution of snow crabs in the Bering Sea, correlated with a northward contraction of cold pool bottom waters (Orensanz et al. 2004). Re-establishment of snow crabs in the southern Bering Sea has been hindered by a concurrent range expansion of one of their predators, Pacific cod, *Gadus macrocephalus,* as bottom temperatures warmed, allowing cod to invade benthic habitats that were previously too cold to occupy (Orensanz et al. 2004, Mueter and Litzow 2008). Expansion of Pacific cod and other commercially fished species (e.g., walleye pollock *Gadus chalcogrammus*, Bering flounder *Hippoglossoides robustus,* and snow crab *Chionoecetes opilio*), which have been historically observed in the Bering Sea, into the Chukchi and Beaufort seas (Rand and Logerwell 2011, Grebmeier 2012), provide evidence of shifting ecosystems in the Alaskan Arctic and sub-Arctic. Because of the strong prominence and ecological role of snow crab in Alaskan Arctic benthic communities (Kolts et al. 2013, Ravelo et al. 2014, 2015, Gross et al. 2016) and the commercial interest in the distribution and biomass of this species (NPFMC 2009), I selected to focus on this species for this dissertation.

Snow crabs dominate biomass and abundance in benthic communities across the Chukchi and western Beaufort Seas (Bluhm et al. 2009, Rand and Logerwell 2011, Ravelo et al. 2014, 2015). Snow crabs are highly mobile predator/ scavengers and consume a large variety of benthic prey, including bivalves, gastropods, polychaetes, ophiuroids, and crustaceans (Wieczorek and Hooper 1995, Lovrich and Sainte-Marie 1997, Kolts et al. 2013). The degree of selectivity of snow crab diets is unknown for populations occurring outside of regions where commercial fisheries occur. However, preliminary evidence suggesting changing distribution, biomass and abundance, at least on the Chukchi shelf, have highlighted the need for increased understanding of snow crab ecology in these regions (Bluhm et al.

2009). Improving the general understanding of the direct and indirect tropic relationships among snow crabs and prey species comprising benthic food webs of the Chukchi and Beaufort seas is increasingly important given the dramatic changes that these regions have undergone in the past decades.

Snow crabs support important commercial fisheries in both the Atlantic and Pacific subpolar regions (Orensanz and Jamieson 1998, Sainte-Marie 1997). Snow crabs are abundant but small (maximum size ~ 75 mm carapace width [CW]) in the Chukchi Sea (Bluhm et al. 2009, Konar et al. 2014, Ravelo et al. 2014, Gross et al. 2016), and are less abundant but occur at large body sizes (> 100 mm CW) in the Beaufort Sea (Rand and Logerwell 2011). Over the past decades in the Bering Sea, declining abundances of snow crabs (Turnock and Rugolo 2012), combined with a northward contraction out of historical fishing grounds (Orensanz et al. 2004, see above), have raised questions about the feasibility of fisheries expansion into previously unfished, Arctic areas of Alaska. Detailed baseline knowledge of critical habitats for commercial species such as snow crabs, is required to provide sufficient habitat protection for this species (Kolts et al. 2013). However, population dynamics and life history data are scarce for snow crabs in regions where they are not commercially fished, such as the Chukchi and Beaufort seas. Gaining a better understanding of the habitat, food web and dietary requirements as well as the population dynamics of snow crabs as a potential Arctic fishery target species is paramount to ensure sound and sustainable management of this resource in the future.

In this study, I investigated snow crab trophic dynamics and stock characteristics in Arctic waters off the Alaska coast. My overarching goal was to provide baseline information regarding snow crab position in the benthic food web, its specific dietary habits, and expand upon limited life-history and population dynamic data in the Chukchi and Beaufort seas. Chapter 1 of my dissertation provided context for snow crab trophic position within benthic food webs across the Beaufort shelf and upper slope using stable $\delta^{13}C$ and $\delta^{15}N$ isotope analysis. While the trophic role of snow crab within the benthic

community has been studied within the Chukchi Sea (Iken et al. 2010, McTigue and Dunton 2014), this was unknown for the Beaufort Sea. Specifically, it is important to resolve benthic food web structure and trophic redundancy (the degree of dietary overlap among taxa within a food web in $\delta^{13}C$–$\delta^{15}N$ space) across the hydrographically and bathymetrically complex Beaufort shelf and upper slope, and then place snow crab into these systems where they occur.

Expanding upon this trophic baseline in chapter 2 of my dissertation, I then investigated the detailed diet and trophic position of snow crab using stomach contents and stable $\delta^{13}C$ and $\delta^{15}N$ isotope analyses. I was specifically interested in evaluating regional differences in Arctic snow crab diets across the Chukchi, Alaskan Beaufort, and Canadian Beaufort seas, considering differences in productivity and benthic communities of these regions. As snow crabs are a potential future fisheries target species in the Arctic (NPFMC 2009), spatially explicit trophic information is needed to determine whether snow crabs feed differently among regions and whether snow crab removal would impact benthic communities differentially, as well.

Finally, in chapter 3, I provided new and revised estimates of Arctic snow crab biomass and abundance, length-weight relationships, size-at-maturity, and fecundity. I also provided updated estimates of biomass, abundance and sustainable yield for comparison with previous estimates established in the Fishery Management Plan for Fish Resources of the Arctic Management Area (e.g., NPFMC 2009, Goddard et al. 2012). This chapter provides new population metrics based on a decade of new and region-specific studies. The three chapters that comprise this dissertation greatly improve our overall understanding of snow crab ecology in the Alaskan Arctic. This information has a wide range of applications, such as informing the selection of snow crab critical habitat in the Arctic Management Area (comprised of the Chukchi and Beaufort seas, NPFMC 2009), or providing biomass and abundance information that may be compared with historical estimates, contribute to monitoring efforts, and aid in

the development of future management strategies.

LITERATURE CITED

Bluhm BA, Iken K, Hardy SM, Sirenko BI, Holladay BA. 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7:269-293

Goddard P, Lauth R, Armistead C. 2012. Results from the 2012 Chukchi Sea bottom trawl survey of bottomfishes, crabs, and other demersal macrofauna. US Dept Commer, NOAA Tech Memo NMFS-AFSC-278. 110 p

Grebmeier JM. 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Ann Rev Marine Sci 4:63-78

Gross J, Konar B, Brey T, Grebmeier JM. 2016. Size frequency distribution, growth, and mortality of snow crab (*Chionoecetes opilio*) and Arctic lyre crab (*Hyas coarctatus*) in the Chukchi Sea from 2009 to 2013. Deep-Sea Res II. In review

Hill V, Cota G. 2005. Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002. Deep-Sea Res II 52:3344-3354

Iken K, Bluhm BA, Dunton K. 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Res II 57:71-85

Kolts JM, Lovvorn JR, North CA, Grebmeier JM, Cooper LW. 2013. Relative value of stomach contents, stable isotopes, and fatty acids as diet indicators for a dominant invertebrate predator (*Chionoecetes opilio*) in the northern Bering Sea. J Exp Mar Biol Ecol 449:274-283

Konar B, Ravelo A, Grebmeier J, Trefry JH. 2014. Size frequency distributions of key epibenthic organisms in the eastern Chukchi Sea and their correlations with environmental parameters. Deep-Sea Res II 102:107-118

Lovrich GA, Sainte-Marie B. 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura; Majidae), and its potential importance to recruitment. J Exp Mar Biol Ecol 211:225-

245

Lovvorn JR, Grebmeier JM, Cooper LW, Bump JK, Richman JG. 2009. Modeling marine protected areas for threatened eiders in a climatically shifting Bering Sea. Ecol Appl 19:1596-1613

McTigue ND, Dunton KH. 2014. Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. Deep-Sea Res II 102:84-96

Moore SE (2008) Marine mammals as ecosystem sentinels. J Mammal 89:534-540

Mueter FJ, Litzow MA. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol Appl 18:309-320

North Pacific Fishery Management Council (NPFMC). 2009. Arctic Fishery Management Plan. Anchorage, Alaska, 158 p

Orensanz JM, Jamieson GS. 1998. The assessment and management of spatially structured stocks: an overview of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Can Special Pub Fish Aquat Sci:441-459

Orensanz JM, Ernst B, Armstrong DA, Stabeno P, Livingston P. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea- an environmental ratchet? CALCOFI Reports 45:65-79

Rand KM, Logerwell EA. 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475-488

Ravelo AM, Konar B, Trefry JH, Grebmeier JM. 2014. Epibenthic community variability in the northeastern Chukchi Sea. Deep-Sea Res II 102:119-131

Ravelo AM, Konar B, Bluhm BA. 2015. Spatial variability of epibenthic communities on the Alaska Beaufort shelf. Polar Biol 38:1783-1894

Renaud PE, Sejr MK, Bluhm BA, Sirenko B, Ellingsen IH. 2015. The future of Arctic benthos: Expansion, invasion, and biodiversity. Prog Oceanog 139:244-257

Sainte-Marie B. 1997. Comment—An improved link between industry, management and science: review of case history of the southwestern Gulf of St. Lawrence snow crab fishery. Can J Fish Aquat Sci 54:496-500

Smith LC, Stephenson SR. 2013. New Trans-Arctic shipping routes navigable by midcentury. Proc Natl Acad Sci USA 110:E1191-E1195

Steele M, Ermold W, Zhang J. 2008. Arctic Ocean surface warming trends over the past 100 years. Geophys Res Lett 35:L02614

Steele M, Zhang J, Ermold W. 2010. Mechanisms of summertime upper Arctic Ocean warming and the effect on sea ice melt. J Geophys Res 11:C11004

Turnock BJ, Rugolo LJ. 2012. DRAFT Stock assessment of eastern Bering Sea snow crab. Accessed 11 February 2016 from: http://www.npfmc.org/wpcontent/PDFdocuments/resources/SAFE/CrabSAFE/912Chapters/snowcrab2012.pdf

Wassmann P. 2011. Arctic marine ecosystems in an era of rapid climate change. Prog Oceanog 90:1-17

Wieczorek SK, Hooper RG. 1995. Relationship between diet and food availability in the snow crab, *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. J Crustac Biol 15:236-24

CHAPTER 1

Regional benthic food web structure on the Alaska Beaufort Sea shelf [1]

Abstract

Trophic structure and resilience of regional benthic food webs were studied on the Alaska Beaufort Sea shelf across three geographic regions: east, central, and west, and two depth ranges: 14-90 m (shallow) and 100-220 m (deep). Carbon and nitrogen isotope ratios were measured from water column and sediment particulate organic matter (POM) as markers of primary food sources and from common benthic invertebrate taxa. Isotopic niche space ($\delta^{13}C - \delta^{15}N$) occupied by benthic taxa provided measures of community-wide trophic redundancy and separation. The $\delta^{13}C$ of water column and sediment POM were patchy but generally indicative of terrestrial input across the shelf, especially near the mouth of the Colville River (< -25.5 ‰). Food web structures in the shallow and deep western Beaufort regions, however, reflected marine carbon inputs, with most consumers occupying intermediate trophic levels (TL) and food webs of intermediate trophic redundancy and separation relative to the other regions. In the central shallow and east regions, the terrestrial carbon found in sediments was mirrored in consumer tissues. The central deep region contained the highest proportions of higher TL taxa, particularly within the predator feeding guild, possibly reflecting resource partitioning of a limited prey spectrum. The comparatively largest isotopic niche space in the central deep region with high trophic niche separation but low trophic redundancy suggests that this region may be most vulnerable to perturbations. This study provides valuable new understanding of benthic food web dynamics in the understudied Alaska Beaufort Sea region and represents a baseline for future comparison.

[1] Divine LM, Iken K, Bluhm BA (2015) Regional benthic food-web structure on the Alaska Beaufort Sea shelf. Marine Ecology Progress Series 531: 15-32.

Introduction

Arctic benthic shelf communities can be hot spots of biomass and contribute considerably to overall secondary production, carbon cycling, and remineralization of nutrients (Grebmeier 2012, Link et al. 2013). High benthic secondary production on ice-covered Arctic shelves results from phytoplankton and sea ice algal production that are often not extensively grazed in the water column because zooplankton communities are still underdeveloped in the early spring when primary production occurs (Carroll & Carroll 2003). Consequently, a large portion of organic carbon is deposited to the seafloor, effectively coupling pelagic production to benthic invertebrate communities (Feder et al.1994, Grebmeier et al. 2006, Grebmeier 2012). These benthic communities provide food for large invertebrates such as snow crabs (*Chionoecetes opilio*; Kolts et al. 2013), fishes (Atkinson & Percy 1992), as well as large bottom-feeding marine mammals such as gray whales (*Eschrichtius robustus*), walrus *(Odobenus rosmarus)*, and bearded seals (*Erignathus barbatus*) (Lowry et al. 2004, Dehn et al. 2007). Climate change driven shifts in the timing and quantity of primary production available for benthic secondary production will likely have profound effects on ecosystem functioning and services (e.g., carbon sequestration, food web support) of benthic communities. Specifically, changes in the timing of sea ice melt and spring phytoplankton production may critically influence the tight pelagic-benthic coupling of Arctic shelves (Hunt & Stabeno 2002, Grebmeier 2012). Long-term shifts in macrobenthic community composition and carbon cycling attributed to the loss of sea ice and changes in primary production regimes have already been observed in the Bering and Chukchi Seas (Grebmeier 2012). To assess the impacts of these shifts on benthic communities, numerous studies have addressed organic matter assimilation pathways in benthic food webs on Alaska's high Arctic shelves (e.g., Chukchi Sea: Iken et al. 2010, Feder et al. 2011, McTigue & Dunton 2013; nearshore Beaufort Sea:

Dunton et al. 1989, 2006, 2012). However, a large portion of the offshore Beaufort shelf food web remains relatively understudied in comparison with the above-mentioned regions of the Alaskan Arctic.

The Alaska Beaufort shelf is a narrow (~80 km wide), near-rectangular shelf situated between two advective shelves, the Chukchi shelf to the west and the Canadian Arctic Archipelago shelf to the east (Fig. 1.1; Dunton et al. 2006). Sea ice dynamics, local winds, and inflows from the oceanic and coastal boundaries result in complex hydrography and cross-shelf heterogeneity in physical characteristics (Pickart 2004, Dunton et al. 2006, Logerwell et al. 2011). Nutrient-rich, low-salinity waters originating in the Bering Sea flow northward along the eastern Chukchi Sea before diverting east around Point Barrow to enter the western Beaufort Sea and continuing eastward along the shelf break in a jet, delivering nutrients and resuspending particulate organic matter (POM) to the western portion of the shelf (Ashjian et al. 2005). In offshore western and central Beaufort regions, these Chukchi waters encounter flows in the opposite direction in the anti-cyclonic, oligotrophic Beaufort Gyre over the Canada Basin (Pickart 2004). POM is also supplied to Beaufort shelf seafloor communities through upwelling events along the shelf break and circulation associated with seafloor bathymetry near Barrow Canyon adjacent to the western Beaufort slope (Fig. 1.1; Okkonen et al. 2009). Over the past two decades, sea ice has been regularly retreating beyond the shelf break (Carmack & Chapman 2003, Weingartner 2008), allowing wind-driven upwelling to become a frequent feature along the shelf break of the Beaufort Sea, potentially increasing the amount of nutrients supplied to the shelf (Tremblay et al. 2011, Pickart et al. 2013).

Freshwater input also supplies organic matter to the Beaufort shelf region. The Colville and Mackenzie rivers together add nearly 350 km^3 of freshwater runoff annually to the central and eastern portions of the Beaufort shelf (Macdonald et al. 2004). Maximum discharge from the larger Mackenzie River occurs over approximately 3 weeks in spring while nearshore waters are still ice-covered

(Macdonald et al. 2004). This discharge delivers more terrestrial carbon than all other Arctic rivers combined (Rachold et al. 2004), which settles into the sediments (Naidu 1974). Satellite images have captured the sediment plume from the Mackenzie extending over 400 km off the shelf (Macdonald et al. 1999). However, the westward extent of the Mackenzie outflow is variable over time and allochthonous nutrient and terrestrial carbon input from the numerous smaller rivers can probably be as important, at least to nearshore (< 20 m depth) Alaska Beaufort food webs (Dunton et al. 2006). Coastal erosion also contributes large amounts of terrestrially-derived carbon to the Alaska portion of the Beaufort shelf (Goñi et al. 2013). Although the importance of terrestrial carbon subsidies, including from the Mackenzie River, to nearshore benthic food webs of the Beaufort Sea has been established (e.g., Parsons et al. 1989, Dunton et al. 2006, 2012), the seaward and lateral extents of the terrestrial carbon supply to the Beaufort Sea shelf system are largely unknown.

Carbon isotopes ($\delta^{13}C$) are a useful marker of such terrestrial food sources, and $\delta^{13}C$ values more positive than -25.5 ‰ have been defined as marine-derived (i.e., phytoplankton) and values more negative than -25.5 ‰ as reflective of terrestrial carbon contributions in the nearshore Beaufort Sea (Dunton et al. 2012). Terrestrially derived organic matter is typically considered to be less labile, and thus less desirable as a primary food source for benthic consumers, than marine derived organic matter (e.g., Dunton et al. 2006, 2012), although the role of bacteria in reworking terrestrial material into a usable form is largely unknown (Garneau et al. 2009). A declining west-to-east gradient in $\delta^{13}C$ isotope values consistent with increasing terrestrial carbon inputs has been established on the Beaufort shelf specifically in nearshore estuarine sediments (Naidu et al. 2000), zooplankton communities (Saupe et al. 1989), some western shallow benthic fauna (< 50 m depth: Dunton et al. 1989, 2006, 2012), and bowhead whales *(Balaena mysticetus)* feeding in the region (Schell et al. 1989). However, much of the

offshore region of the Beaufort shelf benthos remains undocumented regarding the degree of terrestrial carbon contributions and the effects on the benthic food webs.

Similarly, nitrogen ($\delta^{15}N$) isotope ratios can be used to estimate the trophic level (TL) of consumers relative to their food sources. Here, we define trophic structure as the relative numbers of taxa at different trophic levels. By this definition, we interpret a small range and low $\delta^{15}N$ values in consumer tissues within the benthic food web as tight pelagic-benthic coupling (Dunton et al. 2005, Iken et al. 2010). As water depth increases, however, biological and biogeochemical processes (e.g., microbial alteration, hydrolytic enzymatic activity) change the $\delta^{15}N$ of organic matter as it sinks to the benthos and has been suggested to explain water depth-dependent increases in POM and consumer tissue $\delta^{15}N$ values in several oceanic regions (Rau et al. 1991, Mintenbeck et al. 2007). In addition to depth-related trends, large-scale regional differences have been shown with lower $\delta^{15}N$ values of zooplankton and some benthic fauna in the Beaufort Sea relative to those in the Bering and Chukchi seas (Dunton 1985, Dunton et al.1989). Some causes of these regional gradients may be different isotope fractionation processes related to temperature or variation in the isotopic composition of basal carbon and nitrogen sources (Dunton 1985, Dunton et al. 1989). Broad coverage of the understudied offshore Beaufort Sea shelf is necessary to fully elucidate these potential depth-dependent and geographical gradients as they relate to variability in benthic food web structure across the shelf.

Community-wide measures of trophic niche space in $\delta^{13}C$–$\delta^{15}N$ space provide quantitative estimates of the vulnerability or resilience of a community to changes in trophic structure (Bearhop et al. 2004, Layman et al. 2007). Useful metrics in this context include trophic redundancy (the degree of dietary overlap among taxa within a food web in $\delta^{13}C$–$\delta^{15}N$ space), trophic separation (the degree of dietary separation among taxa within a food web, also termed 'trophic diversity'; Layman et al. 2007), and community niche space (total area occupied by all taxa within a standardized range of $\delta^{13}C$ and $\delta^{15}N$

values; see details in Layman et al. 2007). In a food web with low trophic redundancy and high trophic separation, removal of one species from the system (e.g., by climate change, fisheries removal, competitive interactions, or stochastic events) could leave a vacant niche that could not be easily occupied by another consumer, possibly leading to instability within the food web (Layman et al. 2007). In contrast, in a system with high trophic redundancy and low trophic separation, other consumers occupying a similar trophic role could likely compensate for the role of the removed species. While there are limits to these metrics as absolute measures (Hoeinghaus & Zeug 2008), they are useful for relative comparisons among habitats such as regions across the Beaufort Sea shelf.

The purpose of this study was to characterize benthic food web structure on the Alaska Beaufort Sea shelf using stable isotope analysis. Specifically, we tested the following hypotheses: (1) $\delta^{13}C$ and $\delta^{15}N$ isotopic values of water column and bulk sediment POM vary along a west-to-east gradient on the Beaufort Sea shelf, with lower $\delta^{13}C$ and $\delta^{15}N$ values occurring in the eastern Beaufort Sea because of closer proximity to the Mackenzie River outflow. (2) $\delta^{13}C$ values of water column and bulk sediment POM increase along an onshore-offshore gradient and $\delta^{15}N$ values of bulk sediment POM increase with water depth (offshore). Higher POM $\delta^{13}C$ values occur in offshore regions because of greater distance to terrestrial influx (Schell et al. 1989) and in both isotopes because of longer biogeochemical transformation as materials sink to the greater depth at offshore sites (Mintenbeck et al. 2007, France and Peters 2013). As sinking and transformation do not apply to surface water column POM, we did not hypothesize an offshore increase in surface water column POM $\delta^{15}N$ values. (3) Food web length increases from west to east, reflecting a decrease in fresh marine production from west to east and thus a higher dependence on refractory, terrestrial food sources in the east. (4) Overall food web structure varies among regions, with TL occupied by a given feeding guild being higher in the east compared with those in the west; and (5) The trophic redundancy of consumers decreases and trophic separation

increases from west to east, due to weaker pelagic-benthic coupling, and subsequently more niche specialization, in the eastern Beaufort Sea in response to the limited labile food sources available.

Materials and methods

Study area

Field sampling was conducted at 64 stations in the Alaska Beaufort Sea (Fig. 1.2) from 17 August to 2 September 2011 onboard the R/V *Norseman II* within the framework of the Bureau of Ocean Energy Management "BeauFish" program. Sampling stations were aligned along the shelf between -145 °W and -156 °W at water depths between 14 and 220 m (Table S1). As we were interested in large-scale, shelf-wide trophic patterns, we assigned stations to regions (west, central, east, Fig. 1.2), based on a combination of previous sampling areas that were focused on groundfish surveys (Frost & Lowry 1983, Rand & Logerwell 2011), oceanographic conditions, and based on breaks in the sampling scheme. West stations (bounding box: 70.10 °N to 70.90 °N, -144.95 °W to -147.07 °W) included an area that was sampled in 2008 for bottom communities (Logerwell et al. 2011) and is strongly influenced by water masses originating in the Bering and Chukchi Seas, particularly along the shelf break (Okkonen et al. 2011, Pickart et al. 2013). Previous studies qualitatively (Frost & Lowry 1983) and quantitatively (Rand & Logerwell 2011) described the demersal fish and invertebrate communities of the western portion of the Alaska Beaufort Sea. Additionally, the oceanographic habitats of benthic fish and invertebrates in the western Beaufort Sea have been described (Logerwell et al. 2011). The boundaries for the central (70.50 °N to 71.30 °N, -147.28 °W to -151.34 °W) and east (71.16 °N to 71.81 °N, -151.98 °W to -154.98 °W) regions were chosen to separate out the possibly stronger influence of the Mackenzie River in the eastern portion of the Beaufort shelf (Macdonald et al. 2004). Central and west regions were further divided into depth strata based on bathymetry: shallow ($\leq$ 90 m)

and deep (≥ 100 m), based on breaks in station coverage and the presence of the shelf break jet (Fig. 1.1). The east region contained only one deep station (depth of 127 m), which was combined with the shallower stations and, consequently, east represents only one depth zone. It should be noted that all regions (e.g., 'central shallow') refer to the US portion of the Beaufort shelf (see Fig. 1.2). The physical environment of each station was characterized by bottom water temperature and conductivity (salinity) at every station (n= 64) within ~ 5 m of the seafloor using a SeaBird 25 CTD rosette with an integrated SBE 55 Eco-Water sampler. All CTD data were processed by Seth Danielson (University of Alaska Fairbanks). Spearman's rank correlations were used to determine the relationship between environmental data (bottom temperature and salinity, latitude/longitude, water depth) and regional water column and sediment POM $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios (see below) to assess if patterns in isotope ratios were related to environmental parameters.

Isotope sample collection and preparation

Water column POM samples were collected within the upper ~10-20 m, below the surface freshwater lens, to represent the pelagic food source present at the time of sampling. Water column POM was collected from three water samples per station taken from Niskin bottles attached to the CTD rosette. While not true replicates, averaging multiple samples from one station created a more reliable isotopic mean per station from this heterogeneous POM source than a single sample. Water samples were filtered through a pre-combusted 25 mm diameter GF/F filter and visible swimmers were removed. Filters were fumed with saturated HCl vapors for 24 h and subsequently dried at 60° C for 24 h before isotope analysis (see Iken et al. 2010). Bulk sediment POM (n=1 per station) was collected from the top 1 cm of an undisturbed van Veen grab sample (0.1 m^2) into sterile whirl-packs and stored at -20°C until processing. In the home laboratory, sediments were thawed and each sample was mixed thoroughly.

Approximately 1 mL of sediment were treated with 6 N HCl until bubbling ceased, after which samples were rinsed with distilled water until pH was neutral and then freeze-dried before analysis (modified after Thorton & McManus 1994). Water column and sediment POM samples were collected at every station and then averaged among stations within each region for mean regional POM values.

Epifauna were collected using a plumb-staff beam trawl (2.26 m opening, 7 mm net mesh, 4 mm codend mesh). Benthic infauna were collected from trawl hauls and van Veen grabs that were sieved over 1 mm mesh. Van Veen grabs were not quantitatively sampled for infauna; hence, no quantitative community data were available. Trawls were quantitatively sampled for epibenthic community structure but at a coarser taxonomic level than used for this food web study. Therefore, benthic invertebrate taxa that were either abundant at any sampled station or were seen repeatedly at multiple stations within a region were collected on the regional level for food web analysis. Due to analytical limitations, only those benthic taxa that were well represented at the regional level were collected, i.e., rare taxa were not included. Sampling effort in terms of representative taxa per region was similar for all regions, and collections occurred at all stations within each region until all prominent taxa of the regional benthic communities were collected (based on qualitative observations of abundance for each taxa collected). Thus, the collection of benthic taxa for each region was considered representative of those taxa contributing most to benthic abundance and biomass. Some of those taxa were the same among regions, while others were characteristic only for particular regions. Within each region, three to five individuals of common epibenthic and infaunal invertebrate taxa were collected and sorted to species or practical higher taxon level for stable isotope analysis. Taxonomic identifications were conducted by the authors with support of the taxonomic experts listed in the acknowledgments. Taxonomic names were standardized to the World Register of Marine Species (www.marinespecies.org). Taxa were divided into five feeding guilds based on published information: predator, predator/scavenger, suspension, surface

deposit, and sub-surface deposit feeders (Fauchald & Jumars 1979, Feder et al. 1994, 2005, Iken et al. 2010, Appeltans et al. 2012). Individuals were sub-sampled for muscle or body wall when muscle tissue could not be distinguished, to represent a tissue with slow turnover and long-term nitrogen integration (Kaufman et al. 2008, Weems et al. 2012). Whole organisms were used when tissue samples did not yield sufficient mass for isotope analysis (e.g., small amphipods). Samples containing carbonate were treated with 1 N HCl until bubbling ceased, rinsed with DI water and dried at 60° C for 24 h. Lipid content of all tissue samples was removed with repeated use of 2:1 chloroform:methanol because organisms may vary in their concentrations of isotopically lighter lipids (e.g., Sholto-Douglas et al. 1991). Tissue samples were then re-dried at 60° C for 24 h.

Stable isotope sample and data analysis

Samples were analyzed at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with V-PDB and atmospheric N_2 as standards for carbon and nitrogen, respectively. Sample isotopic ratios were expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000,$$

where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Instrument error was < 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Isotopic values for water column POM were compared among regions using the non-parametric Kruskal-Wallis test (α=0.05) based on individual station means in each region, followed by Steel-Dwass post-hoc comparisons because these data violated the parametric assumptions of normality. Isotope values for surface sediment POM adhered to parametric assumptions and were compared using analysis of variance (ANOVA, α=0.05) followed by a Tukey post-hoc test. Additionally, isotope ratios for water

column POM and sediment POM were compared across stations within each region (paired sample t-test, α=0.05).

Trophic levels (TL_c) of consumers, also referred to as trophic positions (Vander Zanden et al. 1997), were determined for each region using the equation:

$$TL_c = (\delta^{15}N_{consumer} - \delta^{15}N_{Sediment\ POM}) / 3.4 + 1,$$

where 3.4 is the assumed mean enrichment in $\delta^{15}N$ between successive, discrete trophic levels (TL) in marine environments (Vander Zanden & Rasmussen 2001, Post 2002). We make a distinction between the two terms used for food web comparisons: trophic level of consumers (TL_c) and trophic level (TL) to separate the calculated trophic position of an individual taxon (e.g., TL_c= 3.3; a continuous measure) from the aggregation of all taxa occupying a discrete trophic level (e.g., TL 3; a categorical measure). Mean TL_c in the five feeding guilds described above met parametric assumptions and were compared among regions using analysis of variance (ANOVA, α=0.05) followed by a Tukey post-hoc test. It should be noted that both water column and sediment POM represent mixtures of sources, including phytoplankton, bacteria, zooplankton carcasses and fecal pellets, and other particulate matter, with large temporal and spatial variation due to biogeochemical processes and turnover times (Cabana & Rasmussen 1996, Tamelander et al. 2006, Sampei et al. 2009). Sediment POM (set as TL=1) was chosen as a baseline for all trophic level calculations because it represents a longer term (i.e., weeks to months) measure of the organic matter available to consumers than water column POM and may better represent the carbon and nitrogen pool in benthic food webs (Cooper et al. 2013). We acknowledge that an unknown amount of microbial processing may render sediment POM at a higher TL than TL1, which we assigned to this source (Baird & Ulanowicz 1989). Water column and sediment POM $\delta^{13}C$ and $\delta^{15}N$ values were plotted in ArcGIS (ESRI, version 10.1, Redlands, CA) by creating triangulated irregular networks (TIN) from vector-based nodes representing station mean values. The TINs are based on an

algorithm that determines which points are most necessary to create an accurate representation of these data (ESRI). Longitude and latitude represented the x- and y-axes, respectively, and either water column or sediment POM $\delta^{13}C$ or $\delta^{15}N$ represented the z-axis for each plot.

Benthic consumers in each region were plotted in $\delta^{13}C$–$\delta^{15}N$ bi-plot space using the convex hull function in MATLAB (Natick, MA 2010), and all metrics discussed below were calculated using this software. Regional convex hull area was used to compare trophic niche space occupied by benthic communities among regions, using several measures of regional trophic structure (Layman et al. 2007). Although this method cannot be used to infer absolute trophic niche characteristics, it is useful for comparative purposes (Hoeinghaus & Zeug 2008). The trophic niche space occupied by the sampled benthic community in each region was calculated as the percentage of regional total area (TA) compared with a standardized area of the plot. In addition, mean distance to the centroid (CD) and mean nearest neighbor distances (NND) were calculated for taxa in each region from the $\delta^{13}C$–$\delta^{15}N$ bi-plots as measures of trophic separation and trophic redundancy, respectively (Layman et al. 2007). Mean CD was calculated as the mean of the Euclidean distances of all individual taxa to the mean $\delta^{13}C$ and $\delta^{15}N$ value of all taxa within the region, and larger mean CD values indicate higher trophic separation (Layman et al. 2007). The mean NND is the mean of all individual Euclidean distances of each taxon to their nearest neighbor in $\delta^{13}C$–$\delta^{15}N$ bi-plot space, and smaller NND values indicate higher trophic redundancy.

Results

Environmental drivers

None of the environmental drivers (bottom temperature and salinity, latitude/longitude, water depth) were significantly correlated with regional water column and sediment POM $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios ($\rho < 0.23$ and $p > 0.05$ for all).

Hypothesis 1: δ13C and δ15N isotopic values of water column and sediment POM food sources vary along a west-to-east gradient on the Beaufort Sea shelf

There was no consistent longitudinal gradient of regional water column or sediment POM $\delta^{13}C$ or $\delta^{15}N$ values (Table 1.1; Fig. 3, 4). Contrary to our hypothesis, mean regional water column POM $\delta^{13}C$ values were highest in the central shallow region (Table 1.1), which was significantly enriched in ^{13}C compared with all other regions (Wilcoxon signed rank, $p < 0.001$), except the east (Fig. 1.3a). Additionally, the overall ranges of regional POM $\delta^{13}C$ values were essentially identical for water column and sediment (-26.2 to -20.7 ‰ and -26.4 to -20.7 ‰, respectively). Mean sediment $\delta^{13}C$ POM values were either similar or slightly lower within each region relative to mean water column POM $\delta^{13}C$, except in the central shallow, where sediment POM $\delta^{13}C$ values were significantly lower compared with the overlying water column POM (Wilcoxon signed rank, $p < 0.001$). The $\delta^{13}C$ of sediment POM was largely homogeneous among the west and central regions, but higher in a localized portion in the far eastern part of the study area (Fig. 1.3b). Within the central shallow region, stations located near the Colville River delta had the lowest sediment $\delta^{13}C$ values (range: -26.4 to -25.6 ‰; Fig. 1.3b).

Similar to water column and sediment $\delta^{13}C$ POM results, mean water column $\delta^{15}N$ values were similar across all regions (Kruskal-Wallis test, $p > 0.05$), but ranged widely among individual stations (from 1.2–11.2 ‰; Fig. 1.4a). The highest water column POM $\delta^{15}N$ values were observed in the west

deep (6.5 ‰ ± 1.2 sd; Table 1.1). All regions had at least slightly lower sediment POM $\delta^{15}N$ values compared with the respective overlying water column POM $\delta^{15}N$ values. Comparing sediment POM $\delta^{15}N$ across regions, the central shallow was significantly lower in sediment $\delta^{15}N$ compared with all other regions (ANOVA, $p < 0.001$), except the east (Fig. 1.4b).

Hypothesis 2: $\delta^{13}C$ values of water column and sediment POM increase along an onshore-offshore gradient and $\delta^{15}N$ values of sediment POM increase with depth.

There were no onshore-offshore trends in enrichment of mean regional water column or sediment POM $\delta^{13}C$ values (Wilcoxon signed rank test, $p > 0.05$ for all regions; Table 1.1, Fig. 1.3a, b). In contrast to our hypothesis, offshore stations were either not different, or slightly lower in water column and sediment POM $\delta^{13}C$, compared with onshore stations (Fig. 1.3a, b). However, within the central shallow region, a distinct onshore-offshore gradient was apparent in water column POM $\delta^{13}C$ values with highest $\delta^{13}C$ at stations located closest to the Colville River and progressively lower values with increasing distance from the shoreline (Fig. 1.3a). This pattern is masked when stations are pooled for a single regional mean.

In the water column, $\delta^{15}N$ was highest along the shelf break in the northwestern west region, and showed a local peak just offshore of the Colville Delta (Fig. 1.4a). Enrichment of ^{15}N in sediment POM was expected from shallow to deep sites because ^{14}N should be preferentially lost in biological processing as materials sink to greater depths (Parsons et al. 1989). Central and west deep regions were indeed slightly higher in mean sediment $\delta^{15}N$ when compared with their shallower counterparts (Fig. 1.4b), with the central deep region being significantly higher than the central shallow (Tukey post-hoc test, $p = 0.001$).

Hypothesis 3: Food web length increases from west to east.

Consumers covered a wide range of isotopic values and TL_c within and across regions (Table S1), and total food web length varied slightly among regions although no west-to-east increase in food web length was evident (Fig. 1.5, 1.6). The central deep region was the only region with five TL and had a top TL_c of 5.3 (Fig. 1.5, 1.6; the predator/scavenger amphipod, *Stegocephalus* sp.). All other regions were comprised of four TL (Fig. 1.6), with the same amphipod (*Stegocephalus* sp.) being the top consumer in the west deep region at TL_c 4.8 (Table S1). The shallow regions were almost identical with respect to top trophic position value: the west shallow region had a top TL_c of 4.7 (predator/scavenger *Gorgonocephalus eucnemis*) and top trophic positions for the central shallow and east regions were 4.8 (predator/ scavenger *Urasterias lincki*) and 4.7 (suspension-feeding Porifera and predatory sea star *Crossaster papposus*), respectively. Basal consumers (TL_c closest to the POM baseline) for all regions except the west deep were suspension feeders (the bivalve *Liocyma fluctuosa* in west shallow; the bryozoan *Flustra* sp. in central deep; the bivalve *Hiatella arctica* in central shallow; Cumacea in east). The sub-surface deposit feeding bivalve, *Yoldia hyperborea*, was the basal consumer in the west deep.

When consumers within feeding guilds were averaged and examined across regions, mean TL_c for each feeding guild occupied in the two west regions were almost identical and also were similar to consumers in the central deep (Fig. 1.5). Consumers in the predator-feeding guild occupied significantly higher mean TL_c in the central deep than this guild in the central shallow and east (ANOVA, $p= 0.04$). Consumers in the predator/ scavenger-feeding guild occupied significantly higher mean TL_c in the west deep than the east (ANOVA, $p= 0.03$). Suspension, surface deposit, and sub-surface deposit feeding guilds were highly variable and their mean TL_c were not statistically different across regions (Fig. 1.5).

Hypothesis 4: Overall food web structure varies among regions.

Regional trophic structure in terms of relative composition of TL varied among regions and fell into three groups: the west deep and shallow were similar in terms of relative composition of TL, the central deep differed from all other regions, and the central shallow and east were similar (Fig. 1.6). It should be noted that arranging taxa into discrete TL is not an exact representation of these food webs since taxa TL_c are continuously distributed relative to the baseline sediment POM values (as shown in Fig. 1.5). However, this comparison may provide information regarding the relative strength of pelagic-benthic coupling among regions. Relative proportions of taxa within TL were similar between the two west regions, with most taxa (> 76 %) in the west shallow and deep regions occupying intermediate TL (TL 3 and 4), with only ~20 % of TL 2 and one TL 1 taxon in the west deep. In the east and central shallow regions, taxa were generally relatively equally distributed across TL 2 and 3 (> 80 %), and both regions had the same number of TL 4 taxa (n= 6). In addition, the east region had the highest number of TL 1 taxa (n= 5) of all regions.

Trophic structure was most unique in the central deep. This region harbored the least number of taxa in the benthic community to be included in the food web study, had the lowest proportion of TL 2 consumer taxa, and was also the only region with three consumer taxa occupying a fifth TL (*Stegocephalus* sp., *Crossaster papposus*, and *Gorgonocephalus eucnemis*).

Hypothesis 5: The trophic redundancy of consumers decreases and trophic separation increases from west to east.

Our data did not support this hypothesis: trophic redundancy and separation did not follow a west-to-east gradient. Redundancy was lowest in the central deep region (NND= 1.01), followed by the west deep region (NND= 0.65), and was highest and similar in the other, shallower regions (NND=

0.51-0.58; Fig. 1.7). Distance to the centroid (CD), used as a proxy for trophic separation, had an inverse pattern to trophic redundancy. Trophic separation was highest in the central deep (CD= 3.14) and similar among other regions (CD= 2.42-2.58; Fig. 1.7). Community-wide isotopic niche space, represented as the total area (TA) occupied in regional $\delta^{13}C$–$\delta^{15}N$ bi-plots, varied among regions (Fig. 1.7). Total area was lowest in the west deep (19 %), highest in the central deep (37 %) despite the lowest number of taxa contributing to the food web, and was relatively similar for the other regions (22-27 %; Fig. 1.7). The relatively high TA in the central deep region compared with other regions coincided with a wide spread in consumer $\delta^{13}C$ values. The lowest and highest $\delta^{13}C$ extremes in the central deep were occupied by the soft coral *Gersemia rubiformis* (-24.1 ‰) and the brittle star *Ophiura sarsii* (-15.3 ‰), respectively; the amphipod *Stegocephalus* sp. (19.4 ‰) and the sea star *Crossaster papposus* (19.2 ‰) occupied the highest $\delta^{15}N$ values (i.e., see gray regions of Fig. 1.7). The TAs in the central shallow and east regions were characterized by several taxa occupying the depleted carbon and nitrogen space, which was not occupied by any taxa in the other regions (Fig. 1.7). These taxa were mostly bryozoans, ampeliscid amphipods and cumaceans, all of which also occurred in other regions but in isotopically more enriched space.

Discussion

Spatial patterns in food sources

We hypothesized that $\delta^{13}C$ values of water column POM would decrease from west to east, following progressively higher influx of terrestrial carbon from the Colville and Mackenzie rivers. Concurrently, less of the nutrient-rich particles originating from the productive Chukchi Sea (Ashjian et al. 2005) or upwelled waters spilling through Barrow Canyon onto the western Beaufort Sea shelf (Aagaard & Roach 1990) would reach the eastern region. Contrary to our hypothesis, we did not see an

obvious influence of the Mackenzie River on water column POM in the east (Fig. 1.3a). This may be due to pelagic POM samples representing a short term "snapshot" of POM isotopic values, which may not necessarily have a detectable terrestrial signature if circulation patterns at the time of sampling carried discharge away from the study site. Dominant circulation patterns may advect the freshwater discharge mostly farther east onto the Mackenzie shelf and Amundsen Gulf instead of westward onto the eastern and central Alaska Beaufort shelf (O'Brien et al. 2006). Alternatively, or in addition, we did not sample during the time of peak production and diagenetic processes until the time of our sampling may have influenced the stable isotope values of POM (Lehmann et al. 2002). Regular sampling throughout the open water period (late spring through summer) as water column production occurs and is advected into the Beaufort from the Chukchi Sea is necessary to further elucidate the variability of water column POM isotopic signatures observed in these regions.

Results of our sediment POM $\delta^{13}C$ analysis, in contrast, indicated consistent and measurable input of terrestrial carbon to the seafloor across much of the Beaufort Sea shelf as reflected in $\delta^{13}C$ values of mostly $\leq$ -24.5 ‰ (Fig. 1.3b). The sediment $\delta^{13}C$ pattern may be interpreted as a longer-term record of the freshwater inflow delivering terrestrial matter from the Colville and other rivers to the Beaufort Sea shelf, and our results are consistent with large-scale sediment patterns in the region (Naidu et al. 2000, Dunton et al. 2012). In contrast to the patchy patterns observed in water column POM, overall sediment POM $\delta^{13}C$ values were more homogenous across the study regions, with the exception of the outer eastern Beaufort shelf, where a localized area of isotopically enriched, marine signature carbon was observed ($\delta^{13}C$ -22.5 to -20.5 ‰). This patch could have resulted from deposition of local marine primary production resulting from a recent upwelling event (Pickart 2004, Pickart et al. 2011, Tremblay et al. 2011) and subsequent vertical flux of particles to the bottom. Possibly, the outer eastern region may be regularly exposed to localized hydrographic conditions that favor accumulation of marine

POM in the sediment record as known from other areas on the Beaufort Sea shelf (Conlan et al. 2013). Slight sediment $\delta^{13}C$ enrichment can also result from intense microbial biomass production in areas of high POM deposition (Ivanov et al. 2012) and may account for a localized region of enriched sediment carbon. Conversely, we observed low sediment POM $\delta^{13}C$ values in the central shallow region (-26.4 to -25.6 ‰), indicating that while sampling occurred at a time when terrestrial carbon was not detected in the water column, it was found in sediments, highlighting the long-term accumulation of terrestrial carbon in this region (Fig. 1.3b). Settled sea ice algae, which are typically enriched in ^{13}C over phytoplankton (Søreide et al. 2006), may also account for some of the variability observed in sediments but we have no current knowledge of their spatial contribution across the Beaufort Sea shelf and benthic food webs.

The overall range of water column POM $\delta^{15}N$ was more than double the range of sediment POM $\delta^{15}N$ (10 ‰ and 5 ‰, respectively), which may reflect the long-term integration of sediment compared with water column POM. As we suggest for the east region, recent depositional events of high phytoplankton biomass may be locally detected in $\delta^{15}N$ of surface sediments. Sediment POM values can also be isotopically modulated by nitrification and denitrification processes that can vary across shelf scales (Granger et al. 2011). In the Canadian Beaufort Sea, slightly reduced sediment $\delta^{15}N$ signals compared with water column POM on the Mackenzie shelf were attributed to the inflow of terrestrial material and possibly preferential degradation of marine sources over terrestrial sources, leading to a lack of $\delta^{15}N$ enrichment in sediments under river discharge influence (Morata et al. 2008). This could be the case for our study area as well, owing to input from numerous smaller rivers across the region.

In addition to a west-east gradient, we hypothesized that there would be an offshore enrichment of carbon isotopes in water column and sediment POM and an enrichment in nitrogen isotopes in sediment POM from shallow to deeper regions of the Beaufort shelf. Enrichment offshore would be

consistent with an increase in the contribution of marine derived organic matter to the food web at offshore stations. However, overall water column surface POM $\delta^{13}C$ patterns exhibited an opposite trend, with deep regions lower in $\delta^{13}C$ than their shallow counterparts. The lowest water column $\delta^{13}C$ POM values were found in the offshore west and central regions and the highest were observed nearshore in close proximity to the Colville River. This latter pattern is contrary to our expectation that terrestrial material from the Colville River significantly influences the coastal regime during the time of run-off (~May-September, Walker & Hudson 2003). Dunton et al. (2012) found very low suspended particle $\delta^{13}C$ values, accompanied by low salinities (ranging from 10-25), in the Beaufort Sea coastal lagoons, which are indicative of a strong terrestrial signal resulting from the numerous small rivers discharging directly into the lagoons. Our observations of isotopically enriched water column POM in the coastal region suggest a remnant of upwelled water may have been trapped onshore and was captured during our snapshot sampling. Upwelling events reaching far inshore are common and have become more frequent during August and September over the past decade (S.R. Okkonen, University of Alaska Fairbanks, pers. comm.). In the Beaufort Sea, shelf break upwelling is driven predominantly by easterly winds and can persist for many days (Pickart et al. 2013). Frequent easterly winds occurred during the sampling season in August 2011 (www.ndbc.noaa.gov), which provides support for the occurrence of upwelling favorable conditions during sampling.

Biogeochemical reworking of POM as particles sink to great depths would be expected to cause increase in sediment $\delta^{15}N$ values deriving from the preferential release of ^{14}N during breakdown (Parsons et al. 1989, Mintenbeck et al. 2007). Sediment $\delta^{15}N$ POM was higher at deeper than shallower sites even with a lack in corresponding increases of $\delta^{13}C$, at least partially supporting our depth-related hypothesis. Overall, contrasting carbon and nitrogen isotopic signatures are possibly due to a

combination of differential degradation and reworking processes, and the complex and dynamic hydrographic regimes in these regions, which are still being investigated.

Regional patterns in benthic food web structure

Food web length in an ecosystem may be governed by total available energy, energy transfer efficiency, or degree of pelagic-benthic coupling within a system (e.g., Grebmeier & McRoy 1989, Moore et al. 2004). Food web length, therefore, can be used as a proxy for identifying functional diversity, ecosystem functioning, and food web stability (Sterner et al. 1997, Worm et al. 2002, Post 2002, Steiner et al. 2005). The taxa collected during this study were the most common and dominant (by abundance and/or biomass) representatives of the regional benthic communities, and thus we consider our results a comprehensive, albeit incomplete, representation of the regional patterns of benthic trophic structure. We hypothesized total benthic food web length would increase from west to east towards the Mackenzie River delta based on an expected weakening of pelagic-benthic coupling with increased riverine refractory material (Carmack et al. 2004, Dunton et al. 2005, 2012). However, total benthic food web lengths were largely similar among all regions with mostly four TL occupied, even though the individual taxa comprising these food webs varied slightly among regions (Table S2). Hence, river influence in the east does not seem to have the hypothesized effect on overall food web length. Our food web length results support previous findings that Arctic benthic shelf food webs typically contain four trophic levels based on nitrogen isotope evidence (e.g., Iken et al. 2010, Feder et al. 2011, McTigue & Dunton 2013). Marine mammals occasionally add a fifth level (Hobson & Welch 1992), but in our study invertebrates occupied a fifth level only in the central deep area, which is similar to the findings of benthic food web structure in the adjacent deep Canada Basin (Iken et al. 2005). All these taxa also occurred in other regions; hence, these extremes were not driven by species unique to the central deep region.

Although overall food web lengths were similar among regions, we detected the hypothesized differences in proportional distribution of taxa among TL and average TL_c of specific feeding guilds among some regions (Figs. 1.5, 1.6). It should be noted that these results are based on taxon presence only and not on biomass, which would represent quantitative contributions to food web structure and thus energy flow, but biomass data were not available at the taxonomic level used in the present study. While future work should include quantitative measures into food web analysis, we can infer differences in basal food sources and perhaps differences in prey availability across regions from our current results. Feeding guild-specific differences were observed at higher TL. For example, predators occupied generally higher TL_c in the central deep than in the central shallow and east regions. Given the close proximity of these regions to each other, the generally lower TL_c of predators in the central shallow and east may indicate the consistent presence and assimilation of terrestrial materials (discussed above) by prey organisms in these regions. The TL_c of predator/scavengers in the west deep was significantly higher than those in the east region, contrasting our hypothesis of a west to east gradient in food web structure due to increasing freshwater input. This pattern may be due to regionally different prey spectra for predators/scavengers, e.g., a large proportion of higher TL taxa in the west deep versus the east (Fig. 1.6), although the east region was not depth stratified and thus limits this comparison. Alternatively, while detrital-based benthic food webs often contain consumers with a high degree of feeding plasticity (Moore et al. 2004, Sweeting et al. 2005, North et al. 2014), selective feeding and particle quality can drive spatial differences in food webs. Regional differences in particle selectivity of suspension and deposit feeders or spatial heterogeneity in detrital particles could be manifested in the higher TL_c of the predator/scavenger guild. Together, our results suggest that particle selectivity may occur at least in some taxa within the suspension, surface deposit and subsurface deposit feeding guilds, and possibly spatial and temporal heterogeneity of particle quality across the shelf at a finer scale than was sampled

in the present study. Similar species-specific differences in deposit-feeders have been found in the Bering Sea with regards to reliance on fresh algal deposits, refractory material and sediment bacteria (North et al. 2014).

In addition to patterns observed in feeding guilds, several regional patterns emerged at the level of trophic redundancy and trophic niche space. The absence of taxa in the highly depleted carbon niche space in the western regions (Fig. 1.7), suggests the prevalence of marine-derived labile and isotopically enriched particles from the Chukchi Sea water masses or upwelling (Weingartner et al. 1998, Pickart et al. 2011). Interestingly, this is not reflected in the sediment POM signatures, perhaps because the fauna quickly consumes and assimilates the labile POM. In contrast, lower TL consumers in the central shallow and east regions utilized a depleted (i.e., terrestrial) carbon source. These taxa in depleted isotopic space were mostly suspension feeders also common to other sampled regions where the depleted carbon sources were either not available or, perhaps more likely, not used by these consumers. Dunton et al. (2012) found similar evidence of a terrestrial carbon subsidy in the nearshore lagoons of the eastern Alaska Beaufort shelf.

The central deep region was set apart from the other regions by a larger isotopic niche space with a food web of high trophic separation and low redundancy, again resembling to some degree the adjacent deep Canada Basin food web (Iken et al. 2005). The central deep region contained the fewest number of taxa overall within the food web, reflecting the low benthic diversity in this region (Konar & Ravelo 2013). The low redundancy in the central deep is likely a result of this low diversity of taxa spread across a large range of TL. This large spread may indicate that these taxa exhibit strong resource partitioning resulting in the lack of niche overlap. As such, the central deep may be more sensitive to natural or anthropogenic disturbances (e.g., fisheries biomass removal, oil and gas activity) than the other regions (Worm & Duffy 2003, Layman et al. 2007). While we do not currently have information

on the food web of the deep eastern Beaufort Sea, we suspect it may be similar to the central deep based on ongoing studies. It generally should be noted that our results are based on the number of taxa present in food webs and not on quantitative measures of biomass or abundance by which these taxa contribute to the food webs, as these data were not available at the same taxonomic resolution as used in the present study. Relating regional food web structure described here to quantitative biomass estimates of these taxa in the various regions could provide additional trophic information.

Conclusions

Establishing a baseline of energy flow and benthic food web structure for future comparisons is critical as Arctic marine environments face unprecedented challenges associated with climate change. Results of this study increase our understanding of food webs on the Alaska Beaufort shelf by documenting the regional-scale similarities and differences in trophic structure and energy flow. Based on our findings we suggest that different regions in the Beaufort Sea may be differentially susceptible to the effects of climatic changes. The west region food webs may be most responsive to hydrographic and oceanographic changes in the inflow of Chukchi Sea water, and consequently, the advection of nutrient-rich particles onto the western Beaufort Sea shelf. We suggest that the central Beaufort Sea shelf and upper slope may be particularly suitable for long-term monitoring, such as conducted in the Bering and Chukchi Seas by the Distributed Biological Observatory (DBO, http://www.arctic.noaa.gov/dbo/). The unique benthic food web characteristics in the central deep region, specifically the high trophic separation and low redundancy of consumers, make this region vulnerable to changes and may serve to provide early detection of biological response to climatic changes.

Acknowledgements

We extend many thanks to the crew of the *R/V Norseman II* for their assistance during the cruise and all cruise participants who were instrumental in sampling efforts. This study was made possible in part by samples collected under BOEM Cooperative Agreement No. M10AC2004 "Beaufort Sea marine Fish Monitoring in the Central Beaufort Sea", U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), Alaska Outer Continental Shelf Region, Anchorage Alaska, as part of the BOEM Environmental Studies Program. The National Science Foundation Marine Ecosystem Sustainability in the Arctic and Subarctic (MESAS) IGERT (Award DGE-0801720) provided support for LD. Participation of KI and BB in the field survey was supported by the Coastal Marine Institute (CMI, Award M11AC00003). Stable isotope analysis was made possible by the North Pacific Research Board (NPRB, Award 1227) and the above CMI grant. We would also like to thank T. Howe and N. Haubenstock of the Alaska Stable Isotope Facility for their assistance during isotope processing. We are grateful for assistance with taxonomic identifications by L. Cole (Smithsonian Institution; ascidians), K. Coyle (University of Alaska Fairbanks (UAF); amphipods), N. Foster (NHF Consulting; mollusks), G. Hendler (Natural History Museum of Los Angeles County; ophiuroids), M. Hoberg (UAF; polychaetes), and C. Mah (Smithsonian Institution; asteroids). K. Arnoult (UAF) assisted with figures created in MATLAB. We are grateful to F. Mueter (UAF), G. Kruse (UAF), and J. Lovvorn (SIU) for critical comments on this manuscript.

References

Aagaard K, Roach TA (1990) Arctic ocean-shelf exchange: Measurements in Barrow Canyon. J Geophys Res 95:18163-18175

Appeltans W, Bouchet P, Boxshall GA, De Broyer C, de Voogd NJ, Gordon DP, Hoeksema BW, Horton T, Kennedy M, Mees J, Poore GCB, Read G, Stöhr S, Walter TC, Costello MJ (eds) (2012) World Register of Marine Species (http://www.marinespecies.org) (accessed 15 Nov 2012)

Ashjian CJ, Gallager SM, Plourde S (2005) Transport of plankton and particles between the Chukchi and Beaufort Seas during summer 2002, described using a Video Plankton Recorder. Deep-Sea Res II 52:3259-3280

Atkinson EG, Percy JA (1992) Diet comparison among demersal marine fish from the Canadian Artic. Polar Biol 11:567-573

Baird D, Ulanowicz RE (1989) The seasonal dynamics of the Chesapeake Bay Ecosystem. Ecol Monogr 59:329-364

Bearhop S, Adams CE, Waldrons S, Fuller RA, MacLeod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007-1012

Cabana G, Rasmussen JB (1996) Comparison of aquatic food chains using nitrogen isotopes. Proc Natl Acad Sci USA 93:10844-10847

Carmack EC, Chapman DC (2003) Wind-driven shelf/basin exchange on an Arctic shelf: The joint roles of ice cover extent and shelf-break bathymetry. Geophys Res Lett 30: doi:10.1029/2003GL017526

Carmack EC, Macdonald RW, Jasper S (2004) Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. Mar Ecol Prog Ser 277:37-50

Carroll ML, Carroll J (2003) The Arctic seas. In: Black KD, GB Shimmield (eds) Biogeochemistry of marine systems, Blackwell, pp 127-156

Conlan K, Hendrycks E, Aitken A, Williams B, Blasco S, Crawford E (2013) Macrofaunal biomass distribution on the Canadian Beaufort Shelf. J Mar Syst 127:76-87

Cooper LW, Sexson MG, Grebmeier JM, Gradinger R, Mordy CW, Lovvorn JR (2013) Linkages between sea-ice coverage, pelagic-benthic coupling, and the distribution of spectacled eiders: Observations in March 2008, 2009 and 2010, northern Bering Sea. Deep-Sea Res II 94:31-43

Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30:167-181

Dunton, KH (1985) Trophic dynamics in marine nearshore systems of the Alaskan high Arctic. PhD dissertation, University of Alaska Fairbanks, Fairbanks, AK

Dunton KH, Saupe SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. Mar Ecol Prog Ser 56:89-97

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic-pelagic coupling in the western Arctic: role of cross-shelf advective processes. Deep-Sea Res II 52:3462-3477

Dunton KH, Weingartner T, Carmack EC (2006) The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food-webs. Prog Oceanogr 71:362-378

Dunton KH, Schonberg SV, Cooper LW (2012) Food-web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuar Coasts 35:416-435

ESRI (2011) Environmental Systems Research Institute: ArcGIS Desktop: Release 10. Redlands, CA

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Ann Rev 17:193-284

Feder HM, Naidu AS, Jewett SC, Hameedi JM, Johnson WR, Whitledge TE (1994) The northeastern Chukchi Sea: benthos-environmental interactions. Mar Ecol Prog Ser 111:171-190

Feder HM, Jewett SC, Blanchard A (2005) Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol 28:402-421

Feder HM, Iken K, Blanchard AL, Jewett SC, Schonberg S (2011) Benthic food web structure in the southeastern Chukchi Sea: an assessment using $\delta^{13}C$ and $\delta^{15}N$ analyses. Polar Biol 34:521-532

Frost KJ, Lowry LF (1983) Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas 1976-1977. US Dept Commerce, NOAA Technical Report, NMFS-SSRF-764, 22 pp

Garneau M-È, Vincent WF, Terrado R, Lovejoy C (2009) Importance of particle-associated bacterial heterotrophy in a coastal Arctic ecosystem. J Marine Syst 75:185-197

Granger J, Prokopenko MG, Sigman DM, Mordy CW, Morse ZM, Morales LV, Sambrotto RN, Plessen B (2011) Coupled nitrification-denitrification in sediment of the eastern Bering Sea shelf leads to ^{15}N enrichment of fixed N in shelf waters. J Geophys Res-Oceans 116:C11006

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Ann Rev Marine Sci 4:63-78

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr 71:331-361

Grebmeier JM, McRoy CP (1989) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Mar Ecol Prog Ser 53:79-91

Goñi MA, O'Connor AE, Kuzyk ZZ, Yunker MB, Gobeil C, Macdonald RW (2013) Distribution and sources of organic matter in surface marine sediments across the North American Arctic margin. J Geophys Res: Oceans 118:4017-4035

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol Prog Ser 84:9-18

Hoeinghaus DJ, Zeug SC (2008) Can stable isotope ratios provide for community-wide measures of trophic structure? Comment. Ecology 89:2353-2357

Hunt GL, Stabeno PJ (2002) Climate change and the control of energy flow in the southeastern Bering Sea. Prog Oceanogr 55:5-22

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Polar Biol 28:238-249

Iken K, Bluhm BA, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Res II 57:71-85

Ivanov MV, Lein AY, Zakharova EE, Savvichev AS (2012) Carbon isotopic composition in suspended organic matter and bottom sediments of the East Arctic Seas. Microbiology 81:645-655

Kaufman MR, Gradinger RR, Bluhm BA, O'Brien DM (2008) Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*. Oecologia 158:11-22

Kolts JM, Lovvorn JR, North CA, Grebmeier JM, Cooper LW (2013) Relative value of stomach contents, stable isotopes, and fatty acids as diet indicators for a dominant invertebrate predator (*Chionoecetes opilio*) in the northern Bering Sea. J Exp Mar Biol Ecol 449:274-283

Konar BL, Ravelo AM (2013) Epibenthic community variability on the Alaskan Beaufort Sea continental shelf. Final Report OCS Study BOEM 2013-01148. Coastal Marine Institute, Fairbanks, Alaska, 48 pp

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42-48

Lehmann MF, Bernasconi SF, Barbieri A, McKenzie JA (2002) Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. Geochim Cosmochim Ac 66:3573-3584

Link H, Piepenburg D, Archambault P (2013) Are hotspots always hotspots? The relationship between diversity, resource and ecosystem functions in the Arctic. PLOS ONE 8:e74077

Logerwell EA, Rand KM, Weingartner TJ (2011) Oceanographic characteristics of the habitat of benthic fish and invertebrates in the Beaufort Sea. Polar Biol 34:1783-1796

Lowry LF, Frost KJ, Burns JJ (2004) Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. J Cetac Res Manage 6:215-223

Macdonald RW, Falkner KK, Swift JH (1999) Connections among ice, runoff and atmospheric forcing in the Beaufort Gyre. Geophys Res Lett 26:2223-2226

Macdonald RW, Naidu AS, Yunker MB, Gobeil C (2004) The Beaufort Sea: distribution, sources, fluxes and burial of organic carbon. In: Stein R, Macdonald RW (eds) The organic carbon cycle in the Arctic Ocean. Springer, pp 177-193

McTigue ND, Dunton KH (2013) Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. Deep-Sea Res II: http://dx.doi.org/10.1016/j.dsr2.2013.07.016

Mintenbeck K, Jacob U, Knust R, Arntz WE, Brey T (2007) Depth-dependence in stable isotope ratio $\delta^{15}N$ of benthic POM consumers: The role of particle dynamics and organism trophic guild. Deep-Sea Res II 54:1015-1023

Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. Ecol Lett 7:584-600

Morata N, Renaud PE, Brugel S, Hobson KA, Johnson BJ (2008) Spatial and seasonal variations in the pelagic-benthic coupling of the southeastern Beaufort Sea revealed by sedimentary biomarkers. Mar Ecol Prog Ser 371:47-63

Naidu AS (1974) Sedimentation in the Beaufort Sea: A synthesis. In: Herman Y (ed) Marine Geology and Oceanography of the Arctic Seas, Springer-Verlag, pp 173-190

Naidu AS, Cooper LW, Finney BP, Macdonald RW, Alexander C, Semiletov IP (2000) Organic carbon isotope ratios ($\delta^{13}C$) of Arctic Amerasian continental shelf sediments. Int J Earth Sciences 89:522-532

North CA, Lovvorn JR, Kolts JM, Brooks ML, Cooper LW, Grebmeier JM (2014) Deposit-feeder diets in the Bering Sea: potential effects of climatic loss of sea ice-related microalgal blooms. Ecol Appl 24:1525-1542

O'Brien MC, Macdonald RW, Melling H, Iseki K (2006) Particle fluxes and geochemistry on the Canadian Beaufort Shelf: Implications for sediment transport and deposition. Cont Shelf Res 26:41-81

Okkonen SR, Ashjian CJ, Campbell RG, Maslowski W, Clement-Kinney JL, Potter R (2009) Intrusion of warm Bering/Chukchi waters onto the shelf in the western Beaufort Sea. J Geophys Res 114:C00A11, doi:10.1029/2008JC004870

Okkonen SR, Ashjian CJ, Campbell RG, Clarke JT, Moore SE, Taylor KD (2011) Satellite observations of circulation features associated with a bowhead whale feeding 'hotspot' near Barrow, Alaska. Remote Sens Environ 115:2168-2174

Parsons TR, Webb DG, Rokeby BE, Lawrence M, Hopky GE, Chiperzak DB (1989) Autotrophic and heterotrophic production in the Mackenzie River/ Beaufort Sea Estuary. Polar Biol 9:261-266

Pickart RS (2004) Shelf break circulation in the Alaskan Beaufort Sea: mean structure and variability. J Geophys Res 109 (C4): C04024

Pickart RS, Spall MA, Moore GWK, Weingartner TJ, Woodgate RA, Aagaard K, Shimada K (2011) Upwelling in the Alaskan Beaufort Sea: atmospheric forcing and local versus non-local response. Prog Oceanogr 88:708-800

Pickart RS, Schulze LM, Moore GWK, Charette MA, Arrigo KR, van Dijken G, Danielson SL (2013) Long-term trends of upwelling and impacts on primary productivity in the Alaskan Beaufort Sea. Deep-Sea Res I 79:106-121

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718

Rachold V, Eicken H, Gordeev VV, Grigoriev MN, Hubberten H-W, Lisitzin AP, Shevchenko VP, Schirrmeister L (2004) Modern terrigenous organic carbon input to the Arctic Ocean. In: Stein R, Macdonald RW (eds.) The organic carbon cycle in the Arctic Ocean. Springer: Heidelberg, pp. 33-55

Rand KM, Logerwell EA (2011) The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475-488

Rau GH, Sullivan CW, Gordon LI (1991) $\delta^{13}C$ and $\delta^{15}N$ variations in Weddell Sea particulate organic matter. Mar Chem 35:355-369

Sampei M, Sasaki H, Hattori H, Forest A, Fortier L (2009) Significant contribution of passively sinking copepods to the downward export flux in Arctic waters. Limnol Oceanogr 54:1894-1900

Saupe SM, Schell DM, Griffiths WB (1989) Carbon-isotope ratio gradients in western arctic zooplankton. Mar Biol 103:427-432

Schell DM, Saupe SM, Haubenstock N (1989) Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}C$ techniques. Mar Biol 103:433-443

Sholto-Douglas AD, Field JG, James AG, van der Merwe NJ (1991) $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios in the Southern Benguela Ecosystem: indicators of food web relationships in different size-classes of plankton and pelagic fish; differences between fish muscle and bone collagen tissues. Mar Ecol Prog Ser 78:23-32

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71:59-87

Steiner CF, Long ZT, Krumins JA, Morin PJ (2005) Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. Ecol Lett 8:819-828

Sterner RW, Bajpai A, Adams T (1997) The enigma of food chain length: absence of theoretical evidence for dynamic constraints. Ecology 78:2258-2262

Sweeting CJ, Jennings S, Polunin NVC (2005) Variance in isotopic signatures as a descriptor of tissue turnover and degree of omnivory. Funct Ecol 19:777-784

Tamelander T, Søreide JE, Hop H, Carroll ML (2006) Fractionation of stable isotopes in the Arctic marine copepod *Calanus glacialis:* Effects on the isotopic composition of marine particulate organic matter. J Exp Mar Biol Ecol 333:231-240

Tremblay JÉ, Bélanger S, Barber DG, Asplin M, Martin J, Darnis G, Fortier L, Gratton Y, Link H, Archambault P, Sallon A, Michel C, Williams WJ, Philippe B, Gosselin M (2011) Climate forcing multiplies biological productivity in the coastal Arctic Ocean. Geophys Res Lett 38: L18604, doi:10.1029/2011GL048825

Vander Zanden JM, Cabana G, Rasmussen JB (1997) Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data. Can J Fish Aquat Sci 54:1142-1158

Vander Zanden JM, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food-web studies. Limnol Oceanogr 46:2061-2066

Walker HJ, Hudson PF (2003) Hydrologic and geomorphic processes in the Colville River delta, Alaska. Geomorphol 56:291-303

Weems J, Iken K, Gradinger R, Wooller MJ (2012) Carbon and nitrogen assimilation in the Bering Sea clams *Nuculana radiata* and *Macoma moesta*. J Exp Mar Biol Ecol 430-431:32-42

Weingartner TJ (2008) Physical Oceanography. In: Hopcroft R, Bluhm B, Gradinger R (eds) Arctic Ocean synthesis: analysis of climate change impacts in the Chukchi and Beaufort Seas with strategies for future research. Institute of Marine Sciences, University of Alaska, Fairbanks, pp 6-17

Weingartner TJ, Cavalieri MD, Aagaard K, Sasaki Y (1998) Circulation, dense water formation and outflow on the northeast Chukchi shelf. J Geophys Res 103:7647-7662

Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. Trends Ecol Evol 18:628-632

Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848-851

Table 1.1. Mean $\delta^{13}C$ and $\delta^{15}N$ isotope values (± 1 sd) for bulk sediment POM (baseline food source) and five consumer feeding guilds. PRED: predator, PS: predator/scavenger, SF: suspension feeder, SDF: surface deposit feeder, SSDF: sub-surface deposit feeder.

Region/ feeding guild	$\delta^{13}C$ ± 1 sd	$\delta^{15}N$ ± 1 sd	mean TL± 1 sd
west deep			
Water column POM	-25.3±0.5	6.5±1.2	
Sediment POM	-25.1±0.5	4.8±1.7	
PRED	-18.8±1.6	14.5±2.4	3.9±0.6
PS	-18.5±1.8	15.2±2.6	4.1±0.8
SF	-19.0±1.0	11.6±2.2	3.0±0.6
SDF	-18.2±0.7	12.0±1.6	3.1±0.5
SSDF	-18.2±1.5	10.9±4.0	2.8±1.2
west shallow			
Water column POM	-24.3±0.8	5.3±0.9	
Sediment POM	-25.3±0.4	4.2±0.4	
PRED	-18.5±1.4	14.1±1.9	3.9±0.5
PS	-19.4±1.3	13.8±2.0	3.8±0.6
SF	-20.0±1.3	11.0±2.6	3.0±0.8
SDF	-18.6±2.3	11.5±1.7	3.2±0.5
SSDF	-19.2±1.5	10.5±2.6	2.8±0.8
central deep			
Water column POM	-24.9±0.4	5.2±1.0	
Sediment POM	-25.0±0.4	4.8±0.6	
PRED	-18.5±0.7	15.7±1.2	4.2±0.7
PS	-19.4±3.1	14.1±3.2	3.7±0.9
SF	-20.0±0.	12.4±3.5	3.2±1.0
SDF	-19.1±1.9	12.5±0.9	3.3±0.3
SSDF	-19.4±2.0	10.4±3.1	2.6±0.9
central shallow			
Water column POM	-23.4±1.1	5.6±1.1	
Sediment POM	-25.5±0.4	3.4±1.1	
PRED	-21.0±3.4	11.7±1.6	3.4±0.5
PS	-20.2±1.4	12.8±1.8	3.8±0.5
SF	-22.3±2.1	8.5±1.9	2.5±0.6
SDF	-20.2±1.0	9.9±1.7	2.9±0.5
SSDF	-20.4±1.2	9.4±1.4	2.8±0.4
east			
Water column POM	-24.2±0.4	5.7±0.7	
Sediment POM	-24.3±0.3	4.4±1.2	
PRED	-20.43±1.3	12.6±2.6	3.4±0.8
PS	-20.9±1.4	12.0±2.0	3.2±0.6
SF	-21.7±0.7	10.4±3.0	2.8±0.9
SDF	-20.8±1.0	10.1±1.6	2.7±0.5
SSDF	-20.6±0.5	9.2±1.5	2.4±0.4

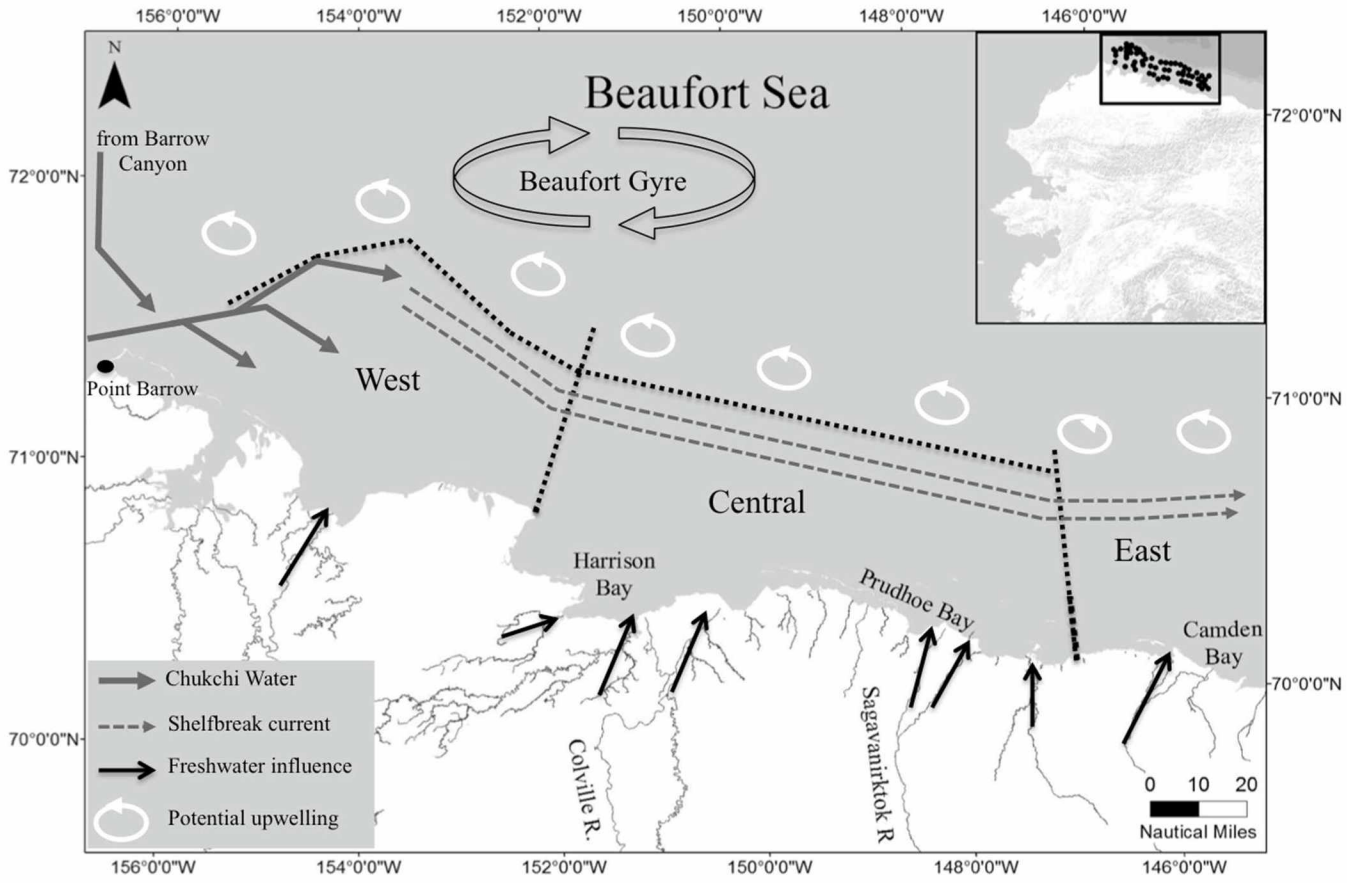

Figure 1.1. The Alaskan Beaufort Sea shelf, from Point Barrow to Camden Bay, Alaska. Major water mass movements are denoted along the Beaufort shelf. Nutrient-rich, low-salinity waters from the Chukchi Sea enter the western Beaufort Sea at Point Barrow and are also funneled through Barrow Canyon adjacent to the slope. In offshore western and central Beaufort regions, waters flow in the opposite direction in the counterclockwise, oligotrophic Beaufort Gyre over the Canada Basin. Upwelling events may occur along any portion of the shelf break during the open water period. Dark dotted lines outline study regions.

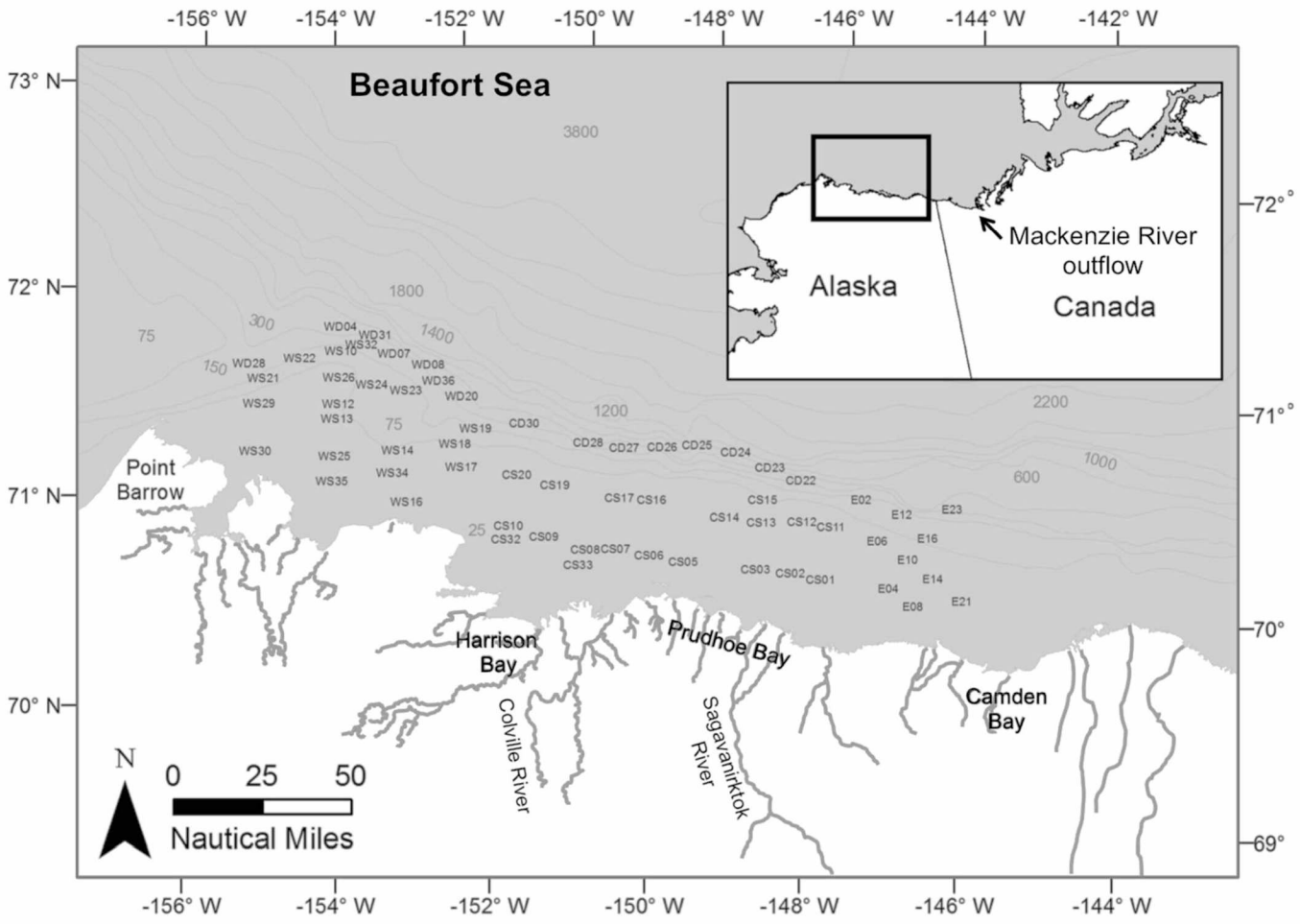

Fig. 1.2. Map of sampling stations, indicated by numbers, in the Alaskan Beaufort Sea (see Table S1). The location of the Mackenzie River outflow is indicated in the smaller map inset and other rivers indicated on map.

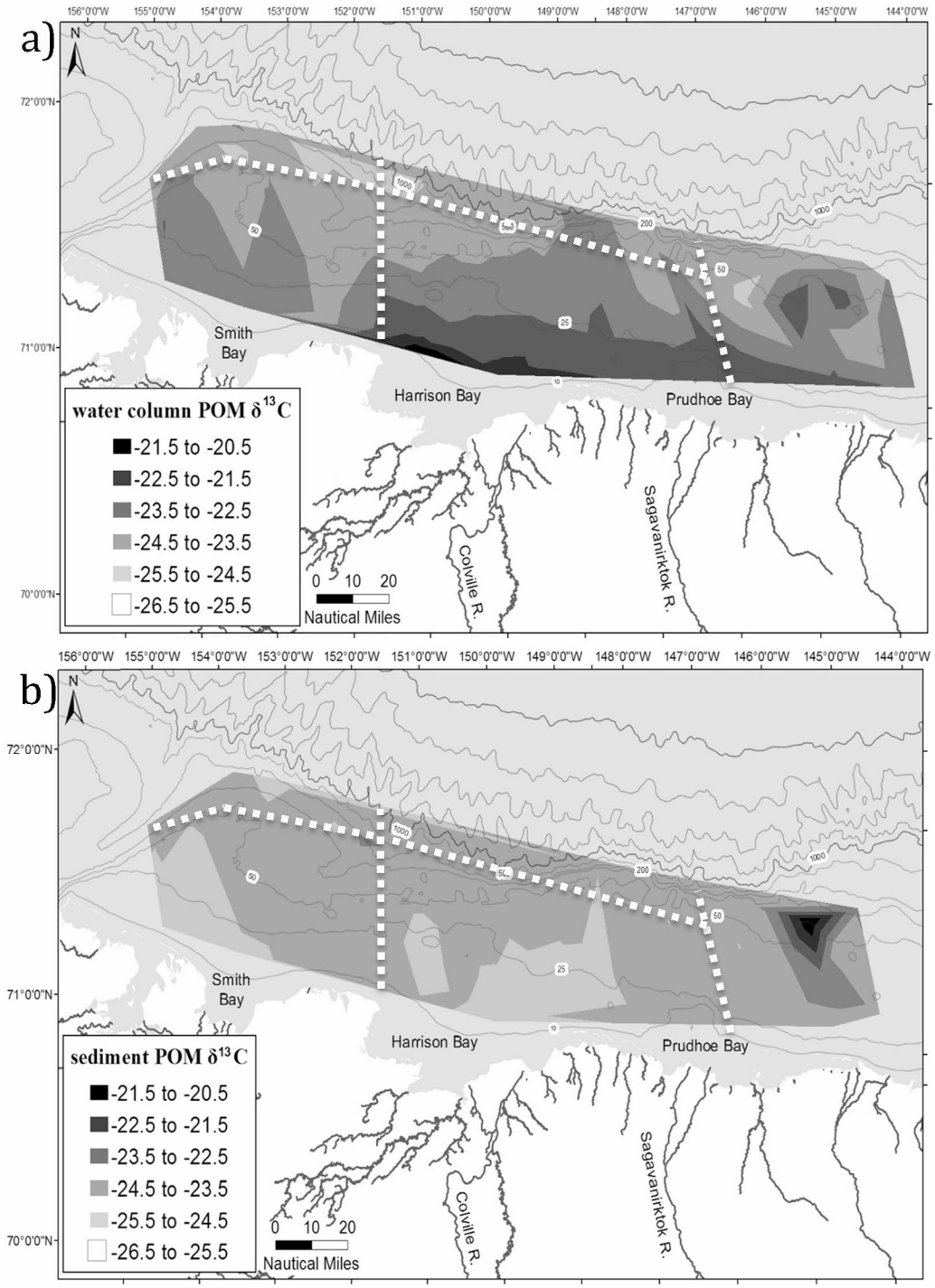

Fig. 1.3. Distribution of $\delta^{13}C$ ‰ (relative to V-PDB) in a) water column POM and b) surface sediment POM of the Alaska Beaufort Sea shelf. Region boundaries are denoted by the white dashed lines. Gray lines and white numbers refer to depth contours (m).

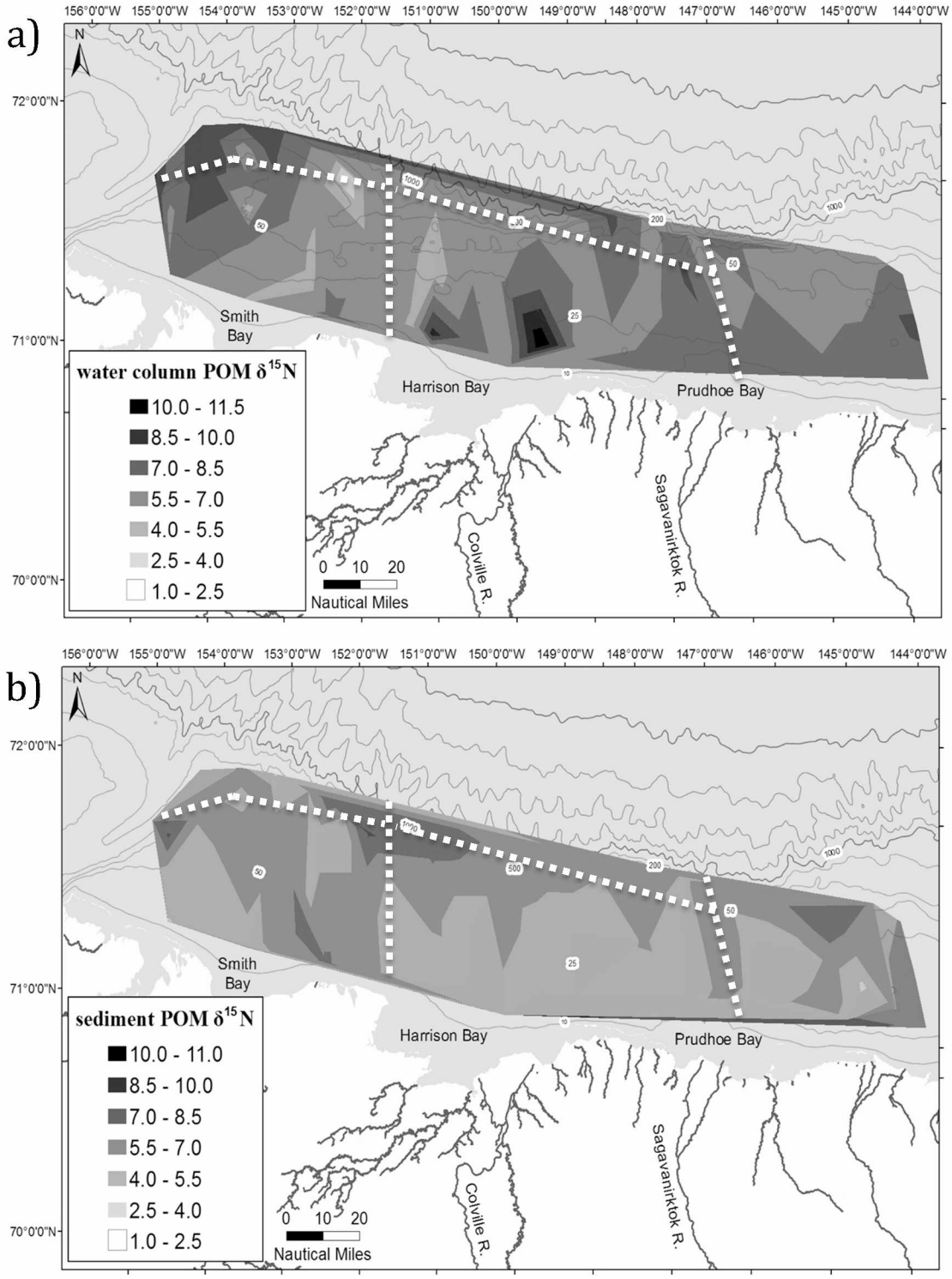

Fig. 1.4. Distribution of $\delta^{15}N$ ‰ (relative to N_{air}) in a) water column POM and b) sediment POM of the Alaska Beaufort Sea shelf. Regions are denoted by the white dashed lines. Gray lines and white numbers refer to depth contours (m).

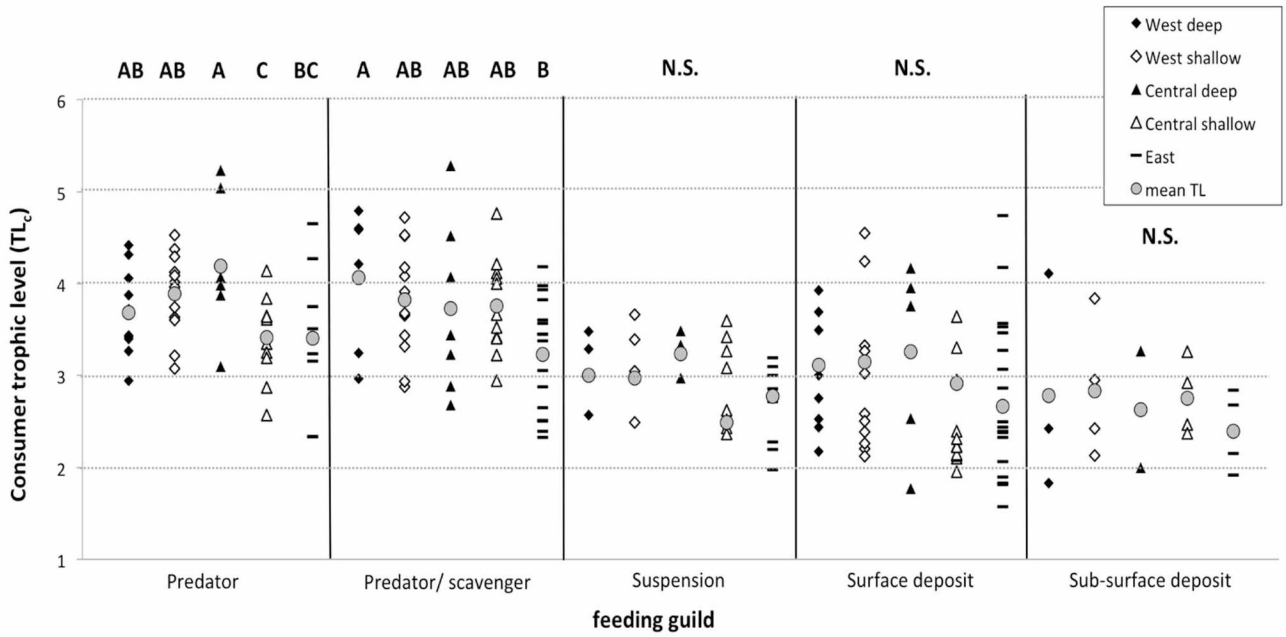

Fig. 1.5. Trophic level of each consumer (TL_c) comprising five dominant feeding guilds across regions of the Alaska Beaufort Sea shelf. All TL values are standardized to regional mean $\delta^{15}N$ of sediment POM as the baseline food source (i.e., sediment POM= TL1). Each data point represents multiple specimens of one species or higher taxon. Gray circles represent mean TL of all consumers within that feeding guild within a region. Letters above data points indicate significant regional differences ($p < 0.05$); N.S.: not significant.

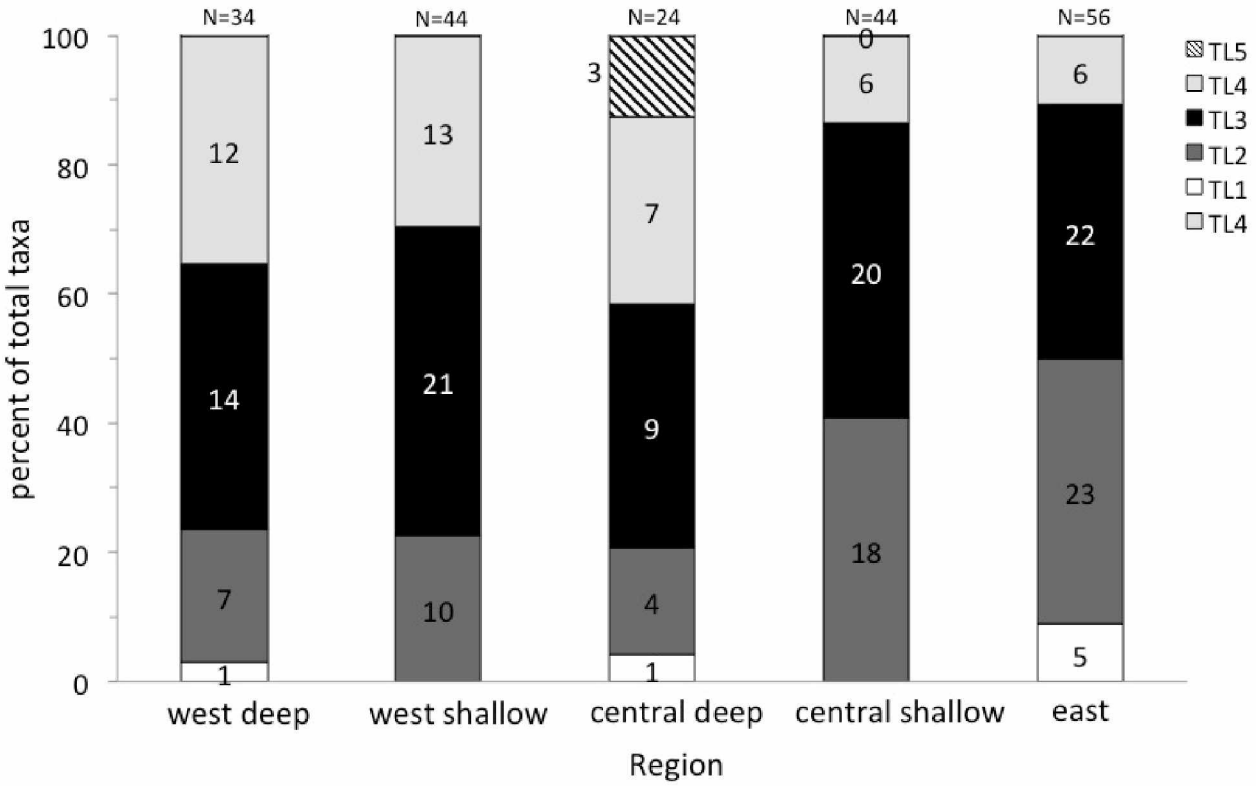

Fig. 1.6. Trophic structure of benthic invertebrates on the Alaska Beaufort Sea shelf across regions with bulk sediment POM as the baseline food source. Values within each bar indicate the total number of taxa in each TL. TL 1 indicates those taxa that are less than a full TL from the baseline value of regional sediment POM. Values at the top of each region bar indicate the total number of taxa collected from the respective region. WD: west deep, WS: west shallow, CD: central deep, CS: central shallow, E: east.

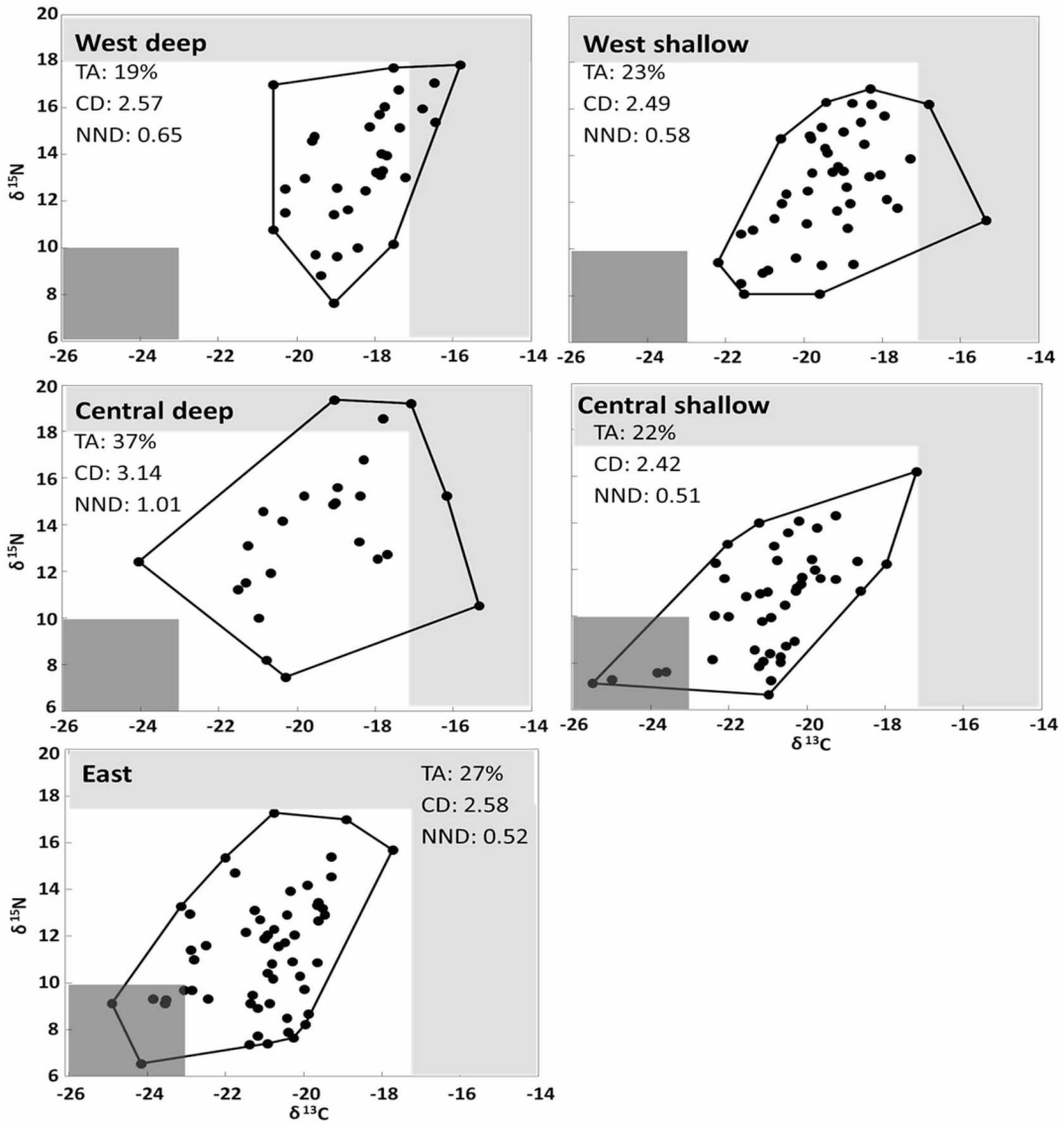

Fig. 1.7. Isotopic niche space as convex hulls of $\delta^{13}C$ and $\delta^{15}N$ spread of benthic invertebrates on the Alaska Beaufort Sea shelf. Light gray regions highlight the presence of high $\delta^{13}C$ and $\delta^{15}N$ values in the west shallow and deep and central deep regions (ranges chosen arbitrarily for illustration purposes only). Dark gray regions in the lower left corners indicate the presence of low $\delta^{13}C$ values in the central shallow and east regions (< -23 ‰, representing terrestrial carbon input; Dunton et al. 2012). TA: total area occupied by a polygon out of the total trophic niche space plotted; CD: mean distance to centroid, indicating trophic separation; NND: mean nearest neighbor distance, indicating trophic redundancy.

CHAPTER 2

Diet analysis of Alaskan Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes [2]

Abstract

We used stomach contents and stable $\delta^{13}C$ and $\delta^{15}N$ isotope analyses to investigate male and female snow crab diets over a range of body sizes (30-130 mm carapace width) in five regions of the Pacific Arctic (southern and northern Chukchi Sea, western, central, and Canadian Beaufort Sea). Snow crab stomach contents from the southern Chukchi Sea were also compared to available prey biomass and abundance. Snow crabs consumed four main prey taxa: polychaetes, decapod crustaceans (crabs, amphipods), echinoderms (mainly ophiuroids), and mollusks (bivalves, gastropods). Both approaches revealed regional differences. Crab diets in the two Chukchi regions were similar to those in the western Beaufort (highest bivalve, amphipod, and crustacean consumption). The Canadian Beaufort region was most unique in prey composition and in stable isotope values. We also observed a trend of decreasing carbon stable isotopes in crabs from the Chukchi to those in the Canadian Beaufort, likely reflecting the increasing use of terrestrial carbon sources towards the eastern regions of the Beaufort Sea from Mackenzie River influx. Cannibalism on snow crabs was higher in the Chukchi regions relative to the Beaufort regions. We suggest that cannibalism may have an impact on recruitment in the Chukchi Sea via reduction of cohort strength after settlement to the benthos, as known from the

[2] Divine LM, Mueter FJ, Bluhm BA, Iken K (2015) Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Deep Sea Research II: doi:10.1016/j.dsr2.2015.11.009

Canadian Atlantic. Prey composition varied with crab size only in some size classes in the southern Chukchi and central Beaufort, while stable isotope results showed no size-dependent differences. Slightly although significantly higher mean carbon isotope values for males in the southern Chukchi may not be driven by a gender-specific pattern but rather be reflective of low sample size. Finally, the lack of prey selection relative to availability in crabs in the southern Chukchi suggests that crabs consume individual prey taxa in relative proportions to prey field abundances. The present study is the first to provide a baseline of the omnivorous role of snow crabs across the entire Pacific Arctic, as well as evidence for cannibalism in the Chukchi Sea. In light of climate change predictions for the Alaskan Arctic, and the potential for future fisheries harvest of snow crabs in this region, continued monitoring of snow crabs, including population and trophic dynamics, is increasingly important to assess snow crab impacts on benthic communities and vice versa.

Introduction

Snow crabs (*Chionoecetes opilio*, O. Fabricius, 1788) are widely distributed across subarctic and arctic regions of the northern parts of the North Pacific and North Atlantic Oceans (Armstrong et al. 2010), where they play important roles in benthic ecosystems. Since 2004, snow crabs have also established a non-native, but self-sustaining, population in the Barents Sea (Alvsvåg et al. 2009, Agnalt et al. 2011). Pacific Arctic snow crabs are considered a panmictic population across their geographic range (Albrecht et al. 2014). They are a major contributor to epibenthic biomass across the Chukchi Sea shelf (Bluhm et al. 2009, Hardy et al. 2011, Blanchard et al. 2013a, b, Ravelo et al. 2014) despite their generally small body sizes on the Chukchi shelf (Konar et al. 2014). Large individuals were recently found on the western

Beaufort Sea shelf where they are also major contributors to biomass (Rand and Logerwell 2011, Ravelo et al. 2015). While commercially fished snow crab populations have been extensively studied over decades (e.g., Tarverdieva 1981, Lefebvre and Brêthes 1991, Lovrich and Sainte-Marie 1997, Squires and Dawe 2003), comparatively little is known about their biology, ecology and role in the non-harvested Pacific Arctic distribution range, including their diet and trophic role.

Snow crabs generally occupy a predatory and scavenging role. Where diet studies have occurred, snow crabs consume a large variety of benthic prey including bivalves, gastropods, polychaetes, ophiuroids, and crustaceans (Bering Sea: Tarverdieva 1981, Kolts et al. 2013a; Chukchi Sea: Feder and Jewett 1978; Sea of Japan: Yasuda 1967, Chuchukalo et al. 2011; western North Atlantic: Lefebvre and Brêthes 1991, Wieczorek and Hooper 1995, Lovrich and Sainte-Marie 1997, Squires and Dawe 2003). In some regions, cannibalism on juveniles, combined with predation on other crab species, also is an important contribution to their diet (Lovrich and Sainte-Marie 1997, Chuchukalo et al. 2011). However, the importance of cannibalism may vary by location and be related to the relative abundance of juveniles compared with abundance and size spectra of other available prey taxa. Ontogenetic diet shifts occur as crabs become larger and acquire larger chelae, allowing them to prey on larger prey items and harder-shelled mollusks and clams (Squires and Dawe 2003, Kolts et al. 2013a).

Snow crabs support lucrative commercial fisheries in the northwest Atlantic (eastern Canada and western Greenland), the Sea of Japan, and the eastern Bering Sea. However, warming trends observed in the Bering Sea over the past three decades have resulted in a northward contraction of the commercially exploited stock out of historical fishing grounds in the southeastern portion (Zheng et al. 2001, Orensanz et al. 2004). The current center of

distribution of snow crabs in the Bering Sea has shifted northward of 60°N (Orensanz et al. 2004, Mueter and Litzow 2008). This northward contraction of snow crabs raises critical questions of dispersal and migration dynamics affecting commercial fishing in the eastern Bering Sea, as well as connectivity among populations in the northern Bering, Chukchi, and Beaufort seas. In addition to the decline of the exploitable snow crab stock in the southeastern Bering Sea, increased open waters of the Arctic due to reductions in sea ice associated with climate warming makes these Arctic regions potentially attractive to fishing (Hollowed et al. 2013). Although fisheries biomass removal is not currently permitted in the Alaskan Arctic, the Arctic Fishery Management Plan lists snow crabs as a potential future fisheries target (NPFMC 2009). In-depth knowledge of snow crab habitat requirements, including dietary preferences and prey availability, is therefore needed for effective fisheries management in this Arctic region.

Snow crabs occupy environmentally complex and disparate regions of the Chukchi and Beaufort seas. The Chukchi shelf is wide and shallow shelf with an average depth of 50 m, with well-documented "hot spots" of high primary production and tight benthic-pelagic coupling that support high benthic standing stocks (Grebmeier et al. 1988, 2006a, b, 2015). Variability in primary production across the shelf is related to the hydrography of several distinct overlying water masses (Walsh et al. 1989). Anadyr Water (AW) delivers high salinity, nutrient-rich waters to the western Chukchi, Alaska Coastal Water (ACW) is comparatively less saline with lower nutrient content in the eastern Chukchi, and the Bering Shelf Water (BSW) of intermediate water properties runs between the AW and ACW (Coachman 1987). Distribution of epibenthic organisms in the Chukchi Sea is structured by sediment characteristics, water depth, and these water masses and their properties, which supply nutrients and carbon to the seafloor through pelagic-benthic coupling (Feder et al. 1994, 2005). Snow crabs on the Chukchi Sea shelf are

members of the epibenthic communities that are typically dominated by crustaceans, echinoderms (mostly ophiuroids), and gastropods (Bluhm et al. 2009, Blanchard et al. 2013a, Ravelo et al. 2014). Snow crab abundance and biomass seem to vary regionally and interannually on the Chukchi shelf (Bluhm et al. 2009, 2015, Ravelo et al. 2014), and crabs occur even in areas where bottom temperatures are below their experimentally defined lower thermal limit ($\leq$ -1°C, Foyle et al. 1989).

In contrast to the Chukchi shelf, the Beaufort shelf is a narrow, interior shelf receiving nutrient-rich water inflow from the Chukchi Sea in the west and more oligotrophic waters to the east (Dunton et al. 2006). Overall benthic biomass and abundance are lower in the Beaufort than the Chukchi Sea, reflecting generally lower primary production in the Beaufort Sea with some exceptions, such as the Cape Bathurst area or upwelling-induced algal blooms (Macdonald et al. 1989, Tremblay et al. 2011). Freshwater runoff and land fast ice limit the abundance and diversity of epifauna and infauna of the nearshore Beaufort Sea to ~25 m depth (Dunton et al. 2005, Ravelo et al. 2015). Epibenthic biomass is highest at the shelf break of the western Beaufort Sea (100-200 m; no deeper locations were sampled, Ravelo et al. 2015); snow crabs are most common at depths of 100-500 m along the western to central Beaufort slope (Rand and Logerwell 2011), where they reach larger sizes than those in the Chukchi Sea including commercial-sized snow crabs (>78 mm carapace width [CW] defined for the Bering Sea stock) collected at depths of > 200 m on the Alaska Beaufort slope (Logerwell et al. 2011, Bluhm et al. 2015).

From other large-bodied crabs, such as red king crabs (*Paralithodes camtschaticus*), it is known that they can have substantial top-down influence on benthic community abundance and composition through their feeding activities (e.g., Jørgensen 2005, Britayev et al. 2010). Vice

versa, snow crabs are themselves can be prey, for example for some fish species (e.g., Livingston et al. 1993). Given the high abundance of snow crab in the Pacific Arctic (Paul et al. 1997, Bluhm et al. 2009, Ravelo et al. 2014, Kolts et al. 2015), their northward range shift (Orensanz et al. 2004), and the mandate to fill knowledge gaps in species of potential commercial interest (NPFMC 2009), our goal was to study snow crab diet and trophic position in the Chukchi and Beaufort seas. Stomach content (SCA) and stable isotope (SIA) analyses are common and complementary methods to address diet composition. SCA can provide high taxonomic resolution and at times, depending on preservation state, size information of prey items that were recently consumed (Hyslop 1980). SCA is a suitable tool to compare diets of crab species occupying similar or different habitats, investigate seasonal diet changes (e.g., Sundet et al. 2000), or ontogenetic shifts in diet composition (Stevens et al. 1982). However, soft bodied, easily digested, or crushed prey organisms are likely to be underestimated in importance (Hyslop 1980) and SCA are snapshots of diet at a given time and location. These limitations of SCA can be at least partially overcome with the complementary use of SIA. Trophic studies based on SIA commonly use $\delta^{13}C$ and $\delta^{15}N$ ratios to identify primary carbon sources and trophic positions of species or higher taxa within a local or regional food web (Post 2002). SIA indicates diet over a longer period, from weeks to months in polar invertebrates depending on turnover time of consumer tissues (Mintenbeck et al. 2007, Kaufman et al. 2008, Weems et al. 2012), and is not limited to recent feeding of the organism (Lovvorn et al. 2013). However, distinguishing relative proportions of specific prey in consumers that eat a variety of taxa that themselves have similar diets (and thus similar isotope values) is difficult using SIA. The combined use of SCA and SIA is a more powerful approach for diet studies than each individual method (e.g., Kolts et al. 2013b).

In the present study, we used the complimentary methods of SCA and SIA to provide insight into the diet composition of male and female snow crabs over a range of body sizes and different benthic environments in the Alaskan Arctic. Specifically, we sought to address the following questions for the Chukchi and Beaufort seas: (1) Do regional differences occur in snow crab diets across the Chukchi and Beaufort seas?, (2) Does body size affect snow crab diets within and across study regions?, (3) Do trophic differences occur among some sex-age classes (male, immature female, mature female) within and across study regions?, and (4) Do snow crabs preferentially select for specific prey types or do they feed on prey in similar relative abundances to the prey's availability in the field?

Methods

Snow crabs of sizes 30-130 mm CW were collected across five geographic regions during several cruises in the Chukchi and Beaufort seas from 2011 to 2013 (Table 2.1, Fig. 2.1). These regions were defined based on a combination of previous sampling schemes, hydrography and circulation, and sample size distribution: southern Chukchi Sea (bounding box: 66.05 to 70.00 °N, 164.14 to 168.50 °W), northern Chukchi Sea (70.50 to 73.00 °N, 157.18 to 168.51 °W), western Beaufort Sea (70.10 to 70.90 °N, 144.95 to 147.07 °W), central Beaufort Sea (70.50 to 71.30 °N, 147.28 to 151.34 °W), and Canadian Beaufort Sea (69.93 to 71.33 °N, 123.49 to 140.40 °W). The Alaska Chukchi Sea was divided into north and south regions at 70°N latitude to correspond with geographic terminology used in previous diet studies (e.g., Iken et al. 2010, Norcross et al. 2015). In addition, hydrographic conditions differ between the two regions: Water masses entering the southern Chukchi Sea through Bering Strait slow and allow advected particles to settle, leading to benthic hotspot regions (Grebmeier et al. 2015). Benthic

communities in the northern Chukchi Sea are driven by the complex hydrography of water around Hanna Shoal, creating a mosaic of depositional and advective microhabitats (Blanchard et al. 2013b). The western and central Alaska Beaufort regions correspond with previous groundfish and benthic invertebrate sampling regions (Frost and Lowry 1983, Rand and Logerwell 2011, Divine et al. 2015). The western Beaufort also is under stronger influence and nutrient-rich particle advection from the Chukchi Sea than the central Beaufort Sea (Ashjian et al. 2005), serving as food source for benthic communities (Divine et al. 2015). The Canadian Beaufort region encompassed stations east of the U.S.-Canadian border. Chukchi Sea snow crabs were collected in July-August 2012 aboard the F/V *Alaska Knight* as part of the Arctic Ecosystem Integrated Survey (Arctic Eis) using either an 83-112 eastern otter trawl (mesh size: 10.2 cm wings and body, 8.9 cm intermediate and codend, 3.2 cm codend liner, Goddard et al. 2014 for trawl operations) or a modified plumb staff beam trawl (PSBT-A, mesh size: 7 mm, 4 mm codend liner; Abookire and Rose 2005). We assume that any potential bias due to differences in sampling gears used in the Chukchi Sea was small and not relevant for the objectives of this study as we obtained a range of crab sizes representative of those observed previously in these regions. Crabs from the U.S. Beaufort Sea were collected in August-September aboard the R/V *Norseman II* during the 2011 BeauFish cruise and in August-September during the 2012 and 2013 U.S.-Canadian Transboundary cruises using the PSBT-A (for additional sampling details see Norcross et al. 2015, Ravelo et al. 2015). Snow crabs from the Canadian Beaufort Sea were collected in 2012 and 2013 aboard the R/V *Frosti* using a modified Atlantic Western IIA otter trawl (mesh size: 1.27 cm cod-end and intermediate liner, A. Majewski [DFO] pers. comm.) as part of the Beaufort Regional Environmental Assessment (Department of Fisheries and Oceans Canada). In all cases, stomachs were removed from crabs

through incisions in the dorsal carapace and preserved in ethanol or 10% buffered formalin until analysis. A muscle sample for SIA was removed from a pereiopod of each crab and dried at 60°C for 24 h. In all cases, crabs were sexed and CW measured using digital calipers to the nearest 0.01 mm.

Stomach content analysis

Stomach contents were removed and placed in a Petri dish for visual inspection under a dissecting microscope (Leica M165) outfitted with a Leica DFC420 camera. Each prey item was photo cataloged for taxonomic verification. Contents were identified to lowest taxonomic level possible and presence or absence of diet items was determined for each crab stomach. The frequency of occurrence (FO) for each prey item was determined as the percentage of all crab stomachs in which a diet item occurred within each region, body size, or sex-age class, depending on category of analysis. Hence, each prey item FO value ranged from 0-100% and was independent of the FO values for all other prey items (Brown et al. 2012). FO for each diet item was first averaged for all crabs within each region (regardless of size or sex-age class), and we compared averages to determine regional differences in means. Then we partitioned crabs by size and sex-age classes and calculated FO for these groups, first by pooling across regions and then by comparing sizes and sex-ages within individual regions. The highly degraded state of many prey items as a result of grinding by the gastric mill in snow crab stomachs precluded enumerating prey items per stomach or measuring the dominant taxa by volume or mass.

Stable isotope analysis

Samples for SIA from pereiopod muscle tissue were dried, and lipids were removed with 2:1 chloroform: methanol because lipids may be depleted in ^{13}C and thus may bias carbon values (Mintenbeck et al. 2007, Logan et al. 2008). Tissue samples were then re-dried at 60° C for 24 h. Samples were analyzed at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with V-PDB and atmospheric N_2 as standards for carbon and nitrogen, respectively. Sample isotope ratios were expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000,$$

where X is ^{13}C or ^{15}N of the crab tissue sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Instrument error was < 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

In situ prey availability

To assess the degree of selectivity in snow crabs diets, we compared a subset of snow crab stomach contents to benthic prey availability. For this purpose, macro-invertebrate abundance (individuals m^{-2}) and biomass data (g C m^{-2}) generated from 0.1 m^2 van Veen grab samples rinsed over 1 mm mesh from the 2012 Russian-American Long-Term Census of the Arctic (RUSALCA) program were provided from five stations in the southern Chukchi Sea (CS17, CL1, CL3R, CS8R, CS12R) by J. Grebmeier and L. Cooper (both U. Maryland). These stations were chosen based on their close proximity to 2012 Arctic Eis stations where snow crabs were collected for stomach content analysis (see Fig. 2.1). No prey information was available for the other regions so that this analysis was only done for the southern Chukchi Sea region. Prey

taxa were grouped at the class level and ranked separately for abundance and biomass from 1 to 10 (1 being highest, 10 the lowest, 0 is absent) at each station (Table 2.2). Frequency of occurrence of prey taxa occurring in snow crab stomachs at the same stations in the southern Chukchi Sea were grouped by the same higher taxa as reported for prey biomass and abundance (see Table 2.2). Prey selectivity was compared only to macro-infaunal prey and not epifaunal prey as infauna comprised most snow crab diet items.

Statistical analysis

We used permutational multivariate analysis of variance (PERMANOVA) at a significance level of α=0.05 for all statistical analyses (PRIMER v7 with PERMANOVA). We determined differences in SCA within and among regions, size groups, and sex-age classes based on presence/absence data analysis in a Jaccard Similarity Index resemblance matrix. For statistical analyses involving crab sizes, crabs were grouped into size classes of 10 mm CW (e.g., the 40 mm CW size class included all crabs with 40.0-49.9 mm CW) based on previous snow crab diet studies (Kolts et al. 2013a). Sex-age groups were male, mature female, and immature females. Males were not separated into immature and mature classes because there was high variability in the ratio of carapace width to chela height, a maturity metric used in other regions, which precluded our ability to confidently determine a CW break for immature versus mature male sizes. Maturity of females was determined based on the shape of the abdominal flap and presence or absence of an egg clutch. Immature and mature females overlapped in their size ranges. We treated region, CW, and sex-age class as fixed factors in the PERMANOVA for both SCA and SIA analyses. Post-hoc pairwise comparisons detailed the differences in diets across CW size classes among regions and within a region. Similarity of Percentages (SIMPER)

analysis determined the prey taxa that contributed most to the differences in diets of the crab size classes within each region. We used non-metric multidimensional scaling (nMDS) plots to visualize the differences in diets of different size classes within those regions where significant differences occurred. Similarly, we investigated regional, size, and sex-age differences in snow crab $\delta^{13}C$ and $\delta^{15}N$ stable isotope values via PERMANOVA. Post-hoc pairwise comparisons were conducted across and within each region to explore which regions contributed to significant differences. Canadian Beaufort crabs were excluded from within-region comparisons because only males were collected in this region.

To rule out potential environmental influences on snow crab diets and stable isotope values that may confound SCA or SIA results, we correlated environmental variables (water depth, bottom-water temperature and salinity) with FO diet data and stable isotope values using the BIO-ENV routine in PRIMER. Ranked prey abundance and biomass data (Table 2.2) were compared with ranked snow crab stomach FO data to determine if crabs were selectively feeding on various prey taxa using non-parametric Mann-Whitney U-tests. Selectivity was defined as a significant difference between ranked prey abundance or biomass *in situ* and rank of prey FO in crab stomachs.

Results

Regional diet patterns

Together, SCA and SIA methods indicated Alaskan Arctic snow crabs are omnivorous and consume a wide variety of benthic invertebrate prey across all study regions. The most frequently occurring diet items across all regions were the polychaete *Cistenides hyperborea* (59.5%), bivalves (57.1%), and 'other polychaete' worms (42.9%). Less frequent prey items

included a variety of crustaceans including amphipods (27.2%) and crabs and shrimps (25.7%), ophiuroids (22.2%), and teleost fishes (7.4%). Other items included unidentifiable tissue parts and sediment particles. Regional differences occurred in snow crab diets as revealed in both SCA and SIA ($p= 0.001$ for both approaches, Table 2.3 and 2.4). Crabs in the southern Chukchi region most frequently fed on bivalves (FO= 61%), followed by *C. hyperborea* (FO= 47%) and amphipods (FO= 31%, Fig. 2.2). Compared with all other regions, crabs in the southern Chukchi had the highest FO for brachyuran crabs (possibly juvenile snow crabs, FO= 23%). Crabs in the northern Chukchi region had a similar diet composition to those in the southern Chukchi, including relative high FO for brachyuran crabs (possibly juvenile snow crabs, FO= 15%). In contrast, brachyuran crabs occurred in less than 5% of stomachs in any of the Beaufort regions (Fig. 2.2). Otherwise, snow crabs in the western Beaufort fed in similar proportions to those in the northern and southern Chukchi regions on bivalves (FO= 60%), 'other polychaetes' (FO= 28%), and amphipods (FO=25%), but had a higher proportion of *C. hyperborea* (FO= 70%) compared with Chukchi regions. Crabs in the central Beaufort region most frequently fed on *C. hyperborea* (FO= 83%), with intermediate consumption frequency of 'other polychaetes', ophiuroids and bivalves (FO= 39%, 29%, and 28%, respectively), and low consumption of teleost fishes and amphipods (FO= 15% and 14%, respectively). Canadian Beaufort Sea crabs were quite different in their stomach contents compared with all other regions (PERMANOVA pair-wise comparison, $p< 0.05$ for all comparisons, Table 3), due mainly to high FO of 'other polychaetes' (FO= 50%), low FO of *C. hyperborea* (FO= 13%) and amphipods (FO= 3%), and several common taxa in other regions being absent in the stomach contents of Canadian Beaufort crabs (e.g., brachyuran crabs, 'other crustaceans').

Stable $\delta^{13}C$ and $\delta^{15}N$ isotope values were also regionally different for snow crabs (PERMANOVA, p= 0.001, Table 2.4, Fig. 2.3). Across all regions, $\delta^{13}C$ ranged from -21.50 ‰ to -15.82 ‰ and $\delta^{15}N$ ranged from 11.71 ‰ to 17.27 ‰ in individual crabs. Canadian Beaufort male crabs (the only sex group sampled in that region) had the lowest $\delta^{13}C$ values and were statistically different from crabs in all other regions (PERMANOVA, $p< 0.01$ for all post-hoc comparisons, Table 2.4, Fig. 2.3). Crabs of all sex-age groups in the central Beaufort region were similar to each other in mean values of both isotopes, and were characterized by slightly lower $\delta^{13}C$ and higher $\delta^{15}N$ values compared with crabs from other regions (significant regional differences in all comparisons [$p< 0.01$], except with the northern Chukchi [p= 0.07]).

Effects of size on snow crab diets

Crab size was a significant factor for SCA only in the interaction between region and size class (PERMANOVA, p= 0.002, Table 2.3). These diets differences among size classes based on SCA only occurred within the southern Chukchi and central Beaufort regions (PERMANOVA pair-wise comparison, p= 0.001 and 0.007, respectively, Table 2.3, Fig. 2.4 and 2.5). In the southern Chukchi, the largest size class of snow crabs examined (80 mm CW) was different from all other size classes within that region (SIMPER analysis; average dissimilarity= 59.3%, Fig. 2.4, Table S3) and most frequently consumed the polychaete *Cistenides hyperborea* (FO= 67%) and had higher FO of the bivalve *Yoldia hyperborea* (FO= 33%) and 'other polychaetes' (FO= 100%) than other size classes. Small crabs (40-60 mm CW) more commonly consumed bivalve sp. 1, bivalve sp. 2, amphipods, and gastropods (Fig. 2.4A and B), as well as ophiuroids, which were absent from the diets of 80 mm CW crabs. Bivalve prey partitioning was seen among crab size classes in the southern Chukchi: *Ennucula tenuis* and bivalve sp. 1 were consumed equally

among all size classes, while *Serripes groenlandicus* and 'other bivalves' (species others than those identified here) were consumed only by small crab size classes. *Yoldia hyperborea* was consumed most commonly by the smallest (40 mm CW) and largest (80 mm CW) size classes (17% and 33%, respectively).

In the central Beaufort, the two smallest size classes examined (50 mm and 60 mm CW) had significantly different stomach content composition compared with each other and most other size classes (PERMANOVA pair-wise comparisons $p < 0.05$, Table 2.3, Fig. 2.5). Dissimilarities of the 50 mm CW class were driven, among other factors, by the lack of 'other polychaetes' and teleost fish parts in their diets (Fig. 2.5A) and low FO of detritus/sand/rocks (FO= 25%). Stomach contents within the 60 mm CW size class were characterized by high FO of ophiuroids (FO= 60%) and detritus/sand/rocks (FO= 100%), relatively low FO of 'other polychaetes' (FO= 20%), and the lack of *Yoldia hyperborea*, gastropods, and other prey taxa compared with other size classes (Fig. 2.5A and B). Several prey taxa were found only in intermediate size classes, such as the bivalve *Y. hyperborea*, gastropods, and teleost parts (Fig. 2.5A). In contrast to effects on SCA, body size was not a significant factor in stable isotope values of snow crabs (PERMANOVA, p= 0.72, Table 2.4).

Effects of sex-age on snow crab diets

SCA generally indicated similar diets for male, mature female, and immature female crabs across all study regions (PERMANOVA, p= 0.72, Table 2.3, Fig. 2.3). Within the southern Chukchi Sea, males were enriched in ^{13}C compared with immature and mature females (Fig. 2.3). SIA indicated sex-age differences in several regions (Table 2.4). Diet of most sex-age groups of the western Beaufort, northern and southern Chukchi Sea were relatively similar,

except for slightly higher $\delta^{13}C$ and $\delta^{15}N$ values in southern Chukchi males (PERMANOVA, $p< 0.01$ for all post-hoc comparisons, Table 2.4, Fig. 2.3). Western Beaufort mature females were characterized by distinctly lower $\delta^{15}N$ values than any other group (~1.0 ‰ lower, Fig. 2.3) but were not statistically different (PERMANOVA, $p= 0.06$ for all post-hoc comparisons, Table 2.4).

In situ prey availability (southern Chukchi region only)

Macro-infaunal prey taxa occurred at similar rank orders in snow crab stomach contents as they did *in situ* in the southern Chukchi Sea ($p> 0.05$), with the exception of Sipuncula ($p= 0.02$ for biomass and abundance) and Nemertea ($p= 0.02$ for biomass, Table 2.5). Sipuncula contributed a large fraction of *in situ* biomass and abundance at one station (ranked 1st in biomass and 6th in abundance, Table 2.2) but was absent in crab stomachs. Nemertea ranked 5th in biomass at one station but was also absent in crab stomachs.

Discussion

Regional diet trends

Together, data from SCA and SIA provided regional diet information that contributes to our understanding of snow crab ecology, trophic level, and resource partitioning on the Alaska Chukchi and Beaufort seas shelves. Overall, snow crabs mostly consumed four main invertebrate prey taxa including polychaetes, crustaceans, bivalves, and ophiuroids; in addition, fish were consumed in low frequencies. The range of main prey groups observed in the present study was consistent with previous diet studies of *Chionoecetes* crabs of similar size range in the Bering Sea (Feder and Jewett 1980, Kolts et al. 2013a), Gulf of Alaska (Jewett and Feder 1983), Cook

Inlet (Paul et al. 1979), and Canadian North Atlantic (Wieczorek and Hooper 1995, Lovrich and Sainte-Marie 1997, Squires and Dawe 2003).

Snow crab diets included members of infaunal and epifaunal communities, both of which are patchily distributed throughout the study area as a consequence of varying combinations of hydrography, sediment properties, food supply and trophic interactions (Bluhm et al. 2009, Iken et al. 2010, Ravelo et al. 2014, 2015, Blanchard and Feder 2014, Whitehouse et al. 2014, Grebmeier et al. 2015). Infaunal abundance and biomass is typically dominated by polychaetes, bivalve mollusks, and amphipod crustaceans across the Chukchi and Beaufort seas (Bilyard and Carey 1979, Grebmeier et al. 2006a, Feder et al. 2007, Blanchard et al. 2013a). Our comparative analysis of stomach contents with macro-infaunal prey in the southern Chukchi region showed that frequency of consumption of these groups as prey is closely related to their availability. This agrees with previous findings in the northern Bering Sea where *Chionoecetes* crabs tend to consume prey in relative proportions to prey abundance in the field (Kolts et al. 2013a). Some occasionally abundant taxa seemed to be consumed less frequently compared with their *in situ* abundance in our study, especially some soft-bodied taxa. We suggest, however, that the lack of Sipuncula and Nemertea in crab stomachs in the southern Chukchi Sea is likely based on the lack of identifiable hard parts in these taxa, which typically leads to underrepresentation in stomach content data (Warwick and Somerfield 2008).

On the northeastern Chukchi shelf, polychaetes, bivalve mollusks, and crustaceans account for > 80% of total macro-infaunal abundance (Schonberg et al. 2014). Each of these taxa also had very high (> 50%) FO in crab stomachs from that region, again suggesting that the main prey items reflect local overall prey abundances. Macro-infaunal data for the Beaufort Sea are sparse and in part date back several decades (e.g., Wacasey et al. 1977, Bilyard and Carey 1979,

Carey et al. 1984) or cover depths where snow crabs do not occur (e.g., < 10 m depth, Dunton et al. 2012). Thus, our ability to interpret snow crab diets in the context of prey availability is limited. The polychaete *C. hyperborea* was a particularly prominent prey item in crabs from the western and central Beaufort Sea, while other polychaetes were the most abundant prey item in crabs from the Canadian Beaufort Sea. Limited available data suggest that polychaete abundance in the central and eastern Beaufort Sea is highest at depths of 200 m along the outer continental shelf, and decreases sharply with increasing depth (Bilyard and Carey 1979, S.M. Hardy, UAF, unpublished data). This coincides well with the depth distribution of crabs on the Beaufort Sea shelf, which are most common along the shelf break and upper slope region (Logerwell et al. 2011). Across the Canadian Beaufort shelf, echinoderms (ophiuroids in particular) and bivalves comprise > 70% total macrofaunal biomass and polychaetes contribute up to ~40% biomass (g ww m^{-2}, Conlan et al. 2008, 2013, Roy et al. 2014). In summary, our results suggest that regional differences in snow crab stomach content observed in the present study likely reflect *in situ* community composition of prominent benthic macro-infaunal prey across the study region.

In addition to high consumption of infaunal prey taxa, snow crab also preyed on epibenthic fauna. Ophiuroids and crustaceans typically dominate abundance and biomass of epibenthic communities in varying proportions across both shelves (Chukchi Sea: Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014; Beaufort Sea: Roy et al. 2014, Ravelo et al. 2015). Ophiuroids account on average for > 40% biomass (g ww m^{-2}) and > 60% abundance in the southeastern and northeastern Chukchi Sea, although with high spatial variability (Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014), and for > 40-90% in biomass (g ww m^{-2}) and abundance on the Beaufort Sea shelf (Roy et al. 2014, Ravelo et al. 2015). Ophiuroids were

common prey items and occurred at equal frequencies in snow crab stomachs in all regions. Despite the clear dominance of ophiuroids in epibenthic communities across the study regions, crabs in all regions consumed a variety of prey taxa, such as polychaetes, bivalves, and amphipods more frequently than ophiuroids. As these more common prey taxa are mostly infaunal, diet results from this current study may indicate that snow crab prey on epifauna taxa mostly opportunistically or that they are a less preferred food item due to their relatively low energy content (Hondolero et al. 2012).

One epifaunal prey group that showed strong regional differences in crab stomachs were brachyuran crabs, which were common prey items especially in Chukchi Sea crabs (FO= 23% and 15% in the southern and northern Chukchi Sea, respectively) but not in Beaufort Sea crabs (FO < 5% for all Beaufort regions). Brachyuran crabs, especially *C. opilio* and the lyre crab *Hyas coarctatus*, are common in the Chukchi Sea (Feder et al. 2005, Bluhm et al. 2009, Blanchard et al. 2013a, Ravelo et al. 2014). Although we could not fully confirm identity from the stomach content fractions, the appearance of fragments seemed to point to juvenile snow crabs as this prey category. This FO may indicate an appreciable amount of cannibalism in the Chukchi Sea. Cannibalistic feeding has been a common occurrence in laboratory studies of snow crabs, with 55% of crabs < 50 mm CW cannibalized by larger crabs (Dutil et al. 1997). Cannibalism has also been observed in populations in the northern Bering Sea (Kolts et al. 2013a), Newfoundland (Wieczorek and Hooper 1995, Squires and Dawe 2003), and the Sea of Japan (Chuchukalo et al. 2011). For example, in the Sea of Japan, crabs were the main single prey item of snow crabs by FO (17.6%) and prey mass (18%, Chuchukalo et al. 2011). In the northern Bering Sea, cannibalism on small juveniles (< 20 mm CW) occurred in localized regions and reached an FO of ~40% in snow crab stomachs (Kolts et al. 2013a). Potentially cannibalized crabs were found

in the stomachs of Chukchi Sea crabs ranging from 30-80 mm CW, while we found little evidence of cannibalism in the larger crabs (90-130 mm CW) of the Beaufort Sea. In the St. Lawrence estuary, cannibalism was also more prominent in smaller snow crab < 50 mm CW than larger adults (Lovrich and Sainte-Marie 1997); thus, the lack of conspecific prey in larger crabs may be due to a prey shift to other larger, perhaps more nutritious, prey items. More likely, however, the regional differences in cannibalism we observed were not based on a size-difference in the predatory crabs but result from there being very few small, juvenile crabs in the Beaufort Sea to serve as prey (Rand and Logerwell 2011, Ravelo et al. 2015), while small crabs are very common in the Chukchi Sea (Konar et al. 2014). In general, intraspecific predation may benefit adolescent snow crabs in the Chukchi Sea directly by increasing food supply and indirectly by reducing competition for resources. Severity of cannibalism is typically density-dependent, with smaller snow crabs at ~15-30 mm CW possibly the most susceptible to cannibalism (Lovrich and Sainte-Marie 1997). Cannibalism has been suggested to regulate recruitment and establish cohort strength during the early stages of snow crab ontogeny (Sainte-Marie et al. 1996, Lovrich and Sainte-Marie 1997) and is known as a significant source of mortality in other crab species (Hines and Ruiz 1995, Fernandez 1999). Cannibalism may be an important part of total mortality in the Chukchi Sea given the high abundances of snow crabs, including young stages (Konar et al. 2014), while it seems a negligible source of mortality in the Beaufort Sea. Cannibalism was not included in a previous assessment of snow crab mortality in the eastern Chukchi Sea (Whitehouse et al. 2014) but, based on results from the present study, should be considered in population dynamics and assessments of possible future snow crab fisheries in the Chukchi Sea.

Regional differences in trophic structure also existed in the time-integrated measure of stable isotope analysis, despite overall high variability in the isotope data within each region. The main regional separation based on SIA was observed between the Chukchi Sea and the central and Canadian Beaufort Sea, similar to the regional diet differences we observed based on SCA. Most of this separation was along the carbon stable isotope axis, which represents differences in basal food sources (DeNiro and Epstein 1978). Benthic food webs along the Alaska Beaufort Sea shelf and upper slope receive more marine carbon in the western Beaufort Sea versus stronger terrestrial carbon inputs in the central Beaufort Sea (Dunton et al. 2012, Divine et al. 2015, Bell 2015), which can be traced by the lighter $\delta^{13}C$ values of the terrestrial carbon sources (Wooller et al. 2007). Therefore, the depleted ^{13}C signal in central and Canadian Beaufort Sea crabs in the present study likely reflects the strong imprint of terrestrial source on the benthic food web in the western part of the Beaufort Sea.

Size and sex-age effects on snow crab diets

Generally, most size and sex-age classes within each region had similar diets with respect to both stomach contents and stable $\delta^{13}C$ and $\delta^{15}N$ isotopes. We found size effects only in SCA and sex-age effects only in SIA. Size-related differences in stomach contents were due to the unique diet composition of the largest size class (80 mm CW) relative to all other sizes for southern Chukchi crabs and diet compositions of the two smallest size classes (50 and 60 mm CW) in the central Beaufort Sea. Crabs > 80 mm CW in the southern Chukchi region did not consume several prey taxa that were common in smaller size classes (e.g., ophiuroids, bivalve sp. 1; both FO= 0%, Table S3). Since > 80 mm CW was the largest size class of crabs encountered in the Chukchi regions, it is possible that we detected a shift in diets with increased body size, as

has been observed in snow crabs in the northern Bering Sea (Kolts et al. 2013a). However, since size-based diet differences occurred only between a few size classes in two regions with no consistent patterns or trends across all regions, the size-based results may be artifacts of the low sample sizes or from binning crabs into 10 mm CW size classes. These factors may also explain the lack of detectable differences in SIA among size classes. Due to the overall narrow ranges of $\delta^{13}C$ and $\delta^{15}N$ isotope values among all crabs and high variability within any size grouping, larger sample sizes would be necessary to detect subtle differences.

In general, all sex-age groups consumed similar diets in the present study. Previous gender-specific SCA studies among similar-sized males and females have produced mixed results at different spatial scales in some regions. For example, no differences were found in the diets of male and female snow crabs of similar sizes in Bonne Bay, Newfoundland (Wieczorek and Hooper 1995), but differences between male and female feeding habits occurred at a larger scale across the northeast Newfoundland shelf (Squires and Dawe 2003). In that area, males consumed more ophiuroids, fish, polychaetes, and clams (considered harder to capture prey items), while females preyed more on easily accessible prey items such as shrimp, gastropods, crabs and sea urchins. In the northern Bering Sea, diets were identical for males and females of similar sizes and in general reflected *in situ* prey availability (Kolts et al. 2013a). Additionally, Lovrich and Sainte-Marie (1997) found males were more likely to engage in cannibalism in the laboratory, but the present study found both males and females consumed smaller snow crabs.

Stable isotope analysis revealed subtle gender-specific diet differences in several regions, despite the lack in gender differences of diets from SCA. Males in the southern Chukchi were enriched in ^{13}C compared with mature and immature females within the same region, but given that the mean $\delta^{13}C$ value for males was within 1 ‰ (considered the range of natural variation,

DeNiro and Epstein 1978) of mean $\delta^{13}C$ values for females in the same region, we suggest that these differences are likely of minor biological importance. Differences in mean isotope values were more variable between sexes in the Beaufort Sea, although not significant because of high variability in a low number of replicates.

Conclusions

Snow crab prey items in the Chukchi and Beaufort seas included common benthic taxa that occur across the study region. Frequency of occurrence of prey taxa differed regionally, with most separation of diets observed between the central and Canadian Beaufort regions. Neither size nor gender was a consistent factor explaining diet differences, and the few differences we found may need to be investigated further with larger sample sizes. Cannibalism was pronounced in the Chukchi Sea but not elsewhere, a pattern that may result from the locally high densities of small snow crabs in the Chukchi Sea relative to the Beaufort Sea. As suggested for other regions (Lovrich and Sainte-Marie 1997), we hypothesize that cannibalism may contribute to regulating recruitment in the Chukchi Sea via intraspecific predation that reduces cohort strength after settlement to the benthos. It may be more important than previously considered for fisheries managers to incorporate this source of mortality into assessments of snow crab population dynamics and estimations of sustainable yields for the Arctic Chukchi Sea population (NPFMC 2009). Given that no prey selectivity was apparent in the southern Chukchi Sea (where statistically tested), the present population of snow crabs seems to impact benthic prey fields equally. Should strong range shifts of large (> 80 mm CW) crabs or substantial increases of snow crab populations occur in the southern Chukchi Sea as some evidence suggests (Feder et al. 2005, Mueter and Litzow 2008, Bluhm et al. 2009), they would likely exert increased top down pressure and have the potential to restructure benthic food webs (e.g., Falk-Petersen et al. 2011,

Dvoretsky and Dvoretsky 2015). Thus, continued monitoring of snow crab life history and population dynamics in the Pacific Arctic region is essential to detect future potential increases in snow crab abundances that may impact the benthic prey communities, and subsequently benthic food web structure. More detailed work on establishing relationships between snow crab diets and prey availability across the entire Alaskan Arctic will allow a better assessment of how potential increases in snow crab populations in the Arctic may impact benthic communities. Conversely, changes in benthic community composition, as predicted with continued climate changes (Grebmeier 2012), may impact snow crabs as a potentially valuable commercial resource in the future.

Acknowledgements

We extend many thanks to the crews of the R/V *Norseman II*, F/V *Alaska Knight*, and R/V *Frosti* for their assistance during cruises and all cruise participants who were instrumental in sampling efforts. This study was made possible in part by samples collected in 2011 in the Beaufort Sea under BOEM Cooperative Agreement No. M10AC2004 "Beaufort Sea Marine Fish Monitoring in the Central Beaufort Sea" (BeauFish), U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), Alaska Outer Continental Shelf Region, Anchorage Alaska, as part of the BOEM Environmental Studies Program. Participation of KI and BB in the BeauFish field survey was supported by the Coastal Marine Institute (CMI, Award M11AC00003). Samples were also collected in the Beaufort Sea under the BOEM Agreement No. M12AC00011 "U.S.-Canada Transboundary Fish and Lower Trophic Communities Project" in 2012 and 2013. Samples in the Chukchi Sea were obtained with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service,

U.S. Department of the Interior under Agreement No. 10-CIAP-010 and under BOEM Cooperative Agreement No. M12AC00009 "Arctic Ecosystem Integrated Survey (Arctic Eis)". Some Chukchi Sea crab and infaunal prey samples were also collected through the 2012 Russian-American Long-Term Census of the Arctic (RUSALCA) cruise with support by the National Oceanic and Atmospheric Administration, NA08OAR4320870 CIFAR Amendment 2. The National Science Foundation Marine Ecosystem Sustainability in the Arctic and Subarctic (MESAS) IGERT (Award DGE-0801720) provided support for LD. Stable isotope analysis was made possible by the North Pacific Research Board (NPRB, Award 1227), the Robert and Kathleen Byrd award, Alaska Sea Grant, and the above CMI grant. We would also like to thank J. Grebmeier and L. Cooper (U. Maryland) for providing prey availability data, T. Howe, N. Haubenstock of the Alaska Stable Isotope Facility, and M. Clark for their assistance during isotope processing. We are grateful for assistance with taxonomic identifications by M. Hoberg (University of Alaska Fairbanks) and Ben Gray (UAF), and lab assistance by C. Lipka and C. Serratos (UAF).

References

Abookire AA, Rose CS (2005) Modifications to a plumb staff beam trawl for sampling uneven, complex habitats. Fish Res 71:247-254

Agnalt AL, Pavlov V, Jørstad KE, Farestveit E, Sundet K (2011) The snow crab, *Chionoecetes opilio* (Decapoda, Majoida, Oregoniidae) in the Barents Sea, pp. 283-300. In: BS Galil, F Clark, JT Carlton (eds.) In the wrong place—alien marine crustaceans: distribution, biology, and impacts. Springer, Dordrecht, pp 283-300

Albrecht GT, Valentin AE, Hundertmark KJ, Hardy SM (2014) Panmixia in Alaskan populations of the snow crab *Chionoecetes opilio* (Malacostraca: Decapoda) in the Bering, Chukchi, and Beaufort Seas. J Crust Biol 34:31-39

Alvsvåg J, Agnalt AL, Jørstad KE (2009) Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. Biol Invasions 11:587-595

Armstrong, DA, McDonald PS, Kruse GH, Hines AH, Orensanz JM (2010) A crab for all seasons: The confluence of fisheries and climate as drivers of crab abundance and distribution. In: GH Kruse, GL Eckert, RJ Foy, RN Lipcius, B Sainte-Marie, DL Stram, D Woodby (eds) Biology and management of exploited crab populations under climate change. Alaska Sea Grant, University of Alaska Fairbanks. doi:10.4027/bmecpcc.2010.05

Ashjian CJ, Gallager SM, Plourde S (2005) Transport of plankton and particles between the Chukchi and Beaufort Seas during summer 2002, described using a Video Plankton Recorder. Deep-Sea Res II 52:3259-3280

Bell L (2015) The influence of terrestrial matter in marine food webs of the Beaufort Sea shelf and slope. MS thesis, University of Alaska Fairbanks, Fairbanks, Alaska, 79 pp

Bilyard GR, Carey AG (1979) Distribution of western Beaufort Sea polychaetous annelids. Mar Biol 54:329-339

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013a) Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008-2010. Cont Shelf Res 67:52-66

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013b) Benthic ecology of the northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009-2010. Cont Shelf Res 67:67-76

Blanchard AL, Feder HM (2014) Interactions of habitat complexity and environmental characteristics with macrobenthic community structure at multiple spatial scales in the northeastern Chukchi Sea. Deep-Sea Res II 102:132-143

Bluhm BA, Iken K, Divine LM (2015) Population assessment of snow crab, *Chionoecetes opilio*, in the Chukchi and Beaufort Seas including oil and gas lease areas. CMI Final Rep M11AC00003, BOEM 2015-029, 31 pp

Bluhm BA, Iken K, Hardy SM, Sirenko BI, Holladay BA (2009) Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7:269-293

Britayev TA, Rzhavsky AV, Pavlova LV, Dvoretskij (2010) Studies on impact of the alien Red King Crab (*Paralithodes camtschaticus*) on the shallow water benthic communities of the Barents Sea. J Appl Ichthyol 26 Suppl. 2:66-73

Brown SC, Bizzarro JJ, Calliet GM, Ebert DA (2012) Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). Environ Biol Fish 95:3-20

Carey AG, Boudrias MA, Kern JC, Ruff RE (1984) Selected ecological studies on continental shelf benthos and sea ice fauna in the southwestern Beaufort Sea. Final Rep Outer Cont Shelf Env Assess Prog, Corvallis Oregon. 648 pp

Chuchukalo VI, Nadtochy VA, Koblikov VA, Borilko OY (2011) Diet and some ecological features of the most widespread commercial crab species in the northwestern Sea of Japan in early spring. Russ J Mar Biol 37:558-569

Coachman LK (1987) Advection and mixing on the Bering-Chukchi Shelves. Component A. Advection and mixing of coastal water on high latitude shelves. ISHTAR 1986 Progress report vol. 1. Institute of Marine Science, University of Alaska Fairbanks pp. 1-42

Conlan K, Aitken A, Hendrycks E, McClelland C, Melling H (2008) Distribution patterns of Canadian Beaufort Shelf macrobenthos. J Mar Syst doi:10.1016/j.jmarsys.2007.10.002

Conlan K, Hendrycks E, Aitken A, Williams B, Blasco S, Crawford E (2013) Macrofaunal biomass distribution on the Canadian Beaufort Shelf. J Mar Syst 127:76-87

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495-506

Divine LM, Iken K, Bluhm BA (2015) Regional benthic food web structure on the Alaska Beaufort Sea shelf. Mar Ecol Prog Ser 531:15-32

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic-pelagic coupling in the western Arctic: role of cross-shelf advective processes. Deep-Sea Res II 54:2906-2918

Dunton KH, Weingartner T, Carmack EC (2006) The nearshore western Beaufort Sea ecosystem: Circulation and importance of terrestrial carbon in arctic coastal food webs. Prog Oceanog 71:362-378

Dunton KH, Schonberg SV, Cooper LW (2012) Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuar Coasts 35:416-435

Dutil JD, Munro J, Peloquin M (1997) Laboratory study of the influence of prey size on vulnerability to cannibalism in snow crab (*Chionoecetes opilio* O. Fabricius, 1780). J Exper Mar Biol Ecol 212:81-94

Dvoretsky AG, Dvoretsky VG (2015) Commercial fish and shellfish in the Barents Sea: Have introduced crab species affected the population trajectories of commercial fish? Rev Fish Biol Fisheries 25:297-322

Falk-Petersen J, Renaud P, Anisimova N (2011) Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea- a review. ICES J Mar Sci 68:479-488

Feder HM, Jewett SC (1978) Survey of the epifaunal invertebrates of Norton Sound, southeastern Chukchi Sea, and Kotzebue Sound. IMS Rep R78-1, Institute of Marine Science, University of Alaska Fairbanks, AK, p 124

Feder HM, Jewett SC (1980) Survey of the epifaunal invertebrates of the southeastern Bering Sea, with notes on the feeding biology of selected species. IMS Rep R78-1, Institute of Marine Science, University of Alaska Fairbanks, AK, p 105

Feder HM, Naidu AS, Jewett SC, Hameedi JM, Johnson WR, Whitledge TE (1994) The northern Chukchi Sea: benthos-environmental interactions. Mar Ecol Prog Ser 111:171-190

Feder HM, Jewett SC, Blanchard A (2005) Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol 28:402-421

Feder HM, Jewett SC, Blanchard AL (2007) Southeastern Chukchi Sea (Alaska) macrobenthos. Polar Biol 30:261-275

Fernández M (1999) Cannibalism in Dungeness crab *Cancer magister*: effects of predator-prey size ratio, density, and habitat type. Mar Ecol Prog Ser 182 221-230

Foyle TP, O'Dor RK, Elner RW (1989) Energetically defining the thermal limits of the snow crab. J Exp Biol 145:371-393

Frost KJ, Lowry LF (1983) Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea. In: PW Barnes, Schell DM, Reimnitz E (eds) The Alaskan Beaufort Sea: ecosystems and environments. Academic Press, Orlando, Florida pp 381-402

Goddard P, Lauth RR, Armistead C (2014) Results of the 2012 Chukchi Sea bottom trawl survey of bottomfishes, crabs, and other demersal macrofauna. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-278, 110 p

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annu Rev Mar Sci 4:63-78

Grebmeier JM, Bluhm BA, Cooper LW, Danielson S, Arrigo K, Blanchard AL, Clark JT, Day RH, Frey KE, Gradinger RR, Kędra M, Konar B, Kuletz KJ, Lee SH, Lovvorn JR, Norcross BL, Okkonen SR (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanog 136:92-114

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006a) Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr 71:331-361

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack ED, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006b) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Grebmeier JM, McRoy CP, Feder HM (1988) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Mar Ecol Prog Ser 48:57-67

Hardy SM, Lindgren M, Konakanchi H, Huettmann F (2011) Predicting the distribution and ecological niche of unexploited snow crab (*Chionoecetes opilio*) populations in Alaskan waters: a first open-access ensemble model. Integr Comp Biol 51:608-622

Hines AH, Ruiz GM (1995) Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. Bull Mar Sci 57:884-901

Hollowed AB, Planque B, Loeng H (2013) Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean. Fish Oceanog 22:355-370

Hondolero D, Bluhm BA, Iken K (2012) Caloric content of dominant benthic species from the northern Bering and Chukchi Seas: historical comparisons and the effects of preservation. Polar Biol 35:637-644

Hyslop EJ (1980) Stomach contents analysis—a review of methods and their application. J Fish Biol 17:411-429

Iken K, Bluhm BA, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep-Sea Res II 57:71-85

Jewett SC, Feder HM (1983) Food of the tanner crab *Chionoecetes bairdi* near Kodiak Island, Alaska. J Crust Biol 3:196-207

Jørgensen LL (2005) Impact scenario for an introduced decapod on Arctic epibenthic communities. Biol Invasions 7:949-957

Kaufman MR, Gradinger RR, Bluhm BA, O'Brien DM (2008) Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*. Oecologia 158:11-22

Kolts JM, Lovvorn JR, North CA, Grebmeier JM, Cooper LW (2013a) Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea. Mar Ecol Prog Ser 483:209-220

Kolts JM, Lovvorn JR, North CA, Grebmeier JM, Cooper LW (2013b) Relative value of stomach contents, stable isotopes, and fatty acids as diet indicators for a dominant invertebrate predator (*Chionoecetes opilio*) in the northern Bering Sea. J Exp Mar Biol Ecol 449:274-283

Kolts JM, Lovvorn JR, North CA, Janout MA (2015) Oceanographic and demographic mechanisms affecting population structure of snow crabs in the northern Bering Sea. Mar Ecol Prog Ser 518:193-208

Konar B, Ravelo A, Grebmeier J, Trefry JH (2014) Size frequency distributions of key epibenthic organisms in the eastern Chukchi Sea and their correlations with environmental parameters. Deep-Sea Res II 102:107-118

Lefébvre LL, Brêthes JCF (1991) Influence de la croissance et de facteurs du milieu sur l'alimentation du crabe des neiges, *Chionoecetes opilio* (O. Fabricius), dans le sud-ouest du golf du Saint-Laurent. Can J Zool 69:489-494

Livingston PA, Ward A, Lang GM, Yang M (1993) Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1987 to 1989. U.S. Dept Commer NOAA Tech Memo NMFS-AFSC-11

Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modeling methods. J Anim Ecol 77:838-846

Logerwell E, Rand K, Weingartner TJ (2011) Oceanographic characteristics of the habitat of benthic fish and invertebrates in the Beaufort Sea. Polar Biol 34:1783-1796

Lovrich GA, Sainte-Marie B (1997) Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura; Majidae), and its potential importance to recruitment. J Exp Mar Biol Ecol 211:225-245

Lovvorn JR, Anderson EM, Rocha AR, Larned WW, Grebmeier JM, Cooper LW, Kolts JM, North CA (2013) Variable wind, pack ice, and prey dispersion affect the long-term adequacy of protected areas for an Arctic sea duck. Ecol Appl 24:396-412

Macdonald RW, Carmack EC, McLaughlin FA, Iseki K, Macdonald DM, O'Brien MC (1989) Composition and modification of water masses in the Mackenzie shelf estuary. J Geophys Res 94:18057-18070

Mintenbeck K, Jacob, Knust R, Arntz WE, Brey T (2007) Depth-dependence in stable isotope ratio $\delta^{15}N$ of benthic POM consumers: The role of particle dynamics and organism trophic guild. Deep-Sea Res II 54:1015-1023

Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol Appl 18:309-320

Norcross BL, Holladay BA, Walker KL, Edenfield LE, (2015) Chapter 3.1. Length-weight-age relationships of demersal fishes on the shelf of the Alaskan Beaufort Sea, In: Central Beaufort Sea Marine Fish Monitoring, Final Rep, OCS Study, BOEM 2015-xxx

North Pacific Fishery Management Council, NPFMC (2009) Fishery Management Plan for Fish Resources of the Arctic Management Area. Anchorage, Alaska, 146 pp

Orensanz J, Ernst B, Armstrong DA, Stabeno P, Livingston P (2004) Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an environmental ratchet? CalCOFI Rep 45:65-79

Paul AJ, Feder HM, Jewett SC (1979) Food of the snow crab, *Chionoecetes bairdi* Rathbun, 1924, from Cook Inlet, Alaska (Decapoda, Majidae). Crustaceana, Suppl No. 5:62-68

Paul JM, Paul AJ, Barber WE (1997) Reproductive biology and distribution of the snow crab from the northeastern Chukchi Sea. Am Fish Soc Symp 19:287-294

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718

Rand KM, Logerwell EA (2011) The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475-488

Ravelo AM, Konar B, Trefry JH, Grebmeier JM (2014) Epibenthic community variability in the northeastern Chukchi Sea. Deep-Sea Res II 102:119-131

Ravelo AL, Konar B, Bluhm BA (2015) Spatial variability of epibenthic communities on the Alaska Beaufort shelf. Polar Biol doi:10.1007/s00300-015-1741-9

Roy V, Iken K, Archambault P (2014) Environmental drivers of the Canadian Arctic megabenthic communities. PloS One 9: e100900. doi:10.1371/journal.pone.0100900

Sainte-Marie B, Sévigny JM, Smith BD, Lovrich GA (1996) Recruitment variability in snow crab *Chionoecetes opilio*: pattern, possible causes, and implications for fishery management. In: Baxter B (ed.) Proceedings of the International Symposium on the Biology, Management, and Economics of crabs from high-latitude habitats. Lowell Wakefield Fish Symp Alaska Sea Grant Rep No 96-02:451-478

Schonberg SV, Clarke JT, Dunton KH (2014) Distribution, abundance, biomass and diversity of benthic infauna in the northeast Chukchi Sea, Alaska: relation to environmental variables and marine mammals. Deep-Sea Res II 102:144-163

Squires HJ, Dawe EG (2003) Stomach contents of snow crab (*Chionoecetes opilio*, Decapoda, Brachyura) from the Northeast Newfoundland Shelf. J Northw Atl Fish Sci 32:27-38

Stevens BG, Armstrong DA, Cusimano R (1982) Feeding habits of the Dungeness crab *Cancer magister* as determined by the index of relative importance. Mar Biol 72:135-145

Sundet JH, Rafter EE, Nilssen EM (2000) Sex and seasonal variation in the stomach content of the red king crab, *Paralithodes camtschaticus* in the southern Barents Sea. Crustacean Issues 12:193-200

Tarverdieva MI (1981) Feeding habits of snow crabs *Chionoecetes opilio* and *Chionoecetes bairdi* in the Bering Sea. Zool Zh 60:991-997

Tremblay JÉ, Bélanger S, Barber DG, Asplin M, Martin J, Darnis G, Fortier L, Gratton Y, Link H, Archmbault P, Sallon A, Michel C, Williams WJ, Pillippe B, Gosselin M (2011) Climate forcing multiplies biological productivity in the coastal Arctic Ocean. Geophys Res Lett 38 doi:10.1029/2011GL048825

Wacasey JW, Atkinson EG, Derick L, Weinstein A (1977) Zoobenthos data from the southern Beaufort Sea, 1971–1975. Fish Mar Serv Res Dev Tech Rep No. 41

Walsh JJ, McRoy CP, Coachman LK, Goering JJ, Nihoul JJ, Whitledge TE, Blackburn TH, Parker PL, Wirick CD, Shuert PG, Grebmeier JM, Springer AM, Tripp RD, Hansell DA, Djenidi S, Deleersnijder E, Henriksen K, Lund BA, Andersen P, Müller-Karger FE, Dean K (1989) Carbon and nitrogen cycling within the Bering/ Chukchi Seas: Source regions for organic matter effecting AOU demands of the Arctic Ocean. Prog Oceanog 22:277-359

Warwick RM, Somerfield PJ (2008) All animals are equal, but some animals are more equal than others. J Mar Biol Ecol 366:184-186

Weems J, Iken K, Gradinger R, Wooller MJ (2012) Carbon and nitrogen assimilation in the Bering Sea clams *Nuculana radiata* and *Macoma moesta*. J Exp Mar Biol Ecol 430-431:32-42

Whitehouse GA, Aydin K, Essington TE, Hunt GL (2014) A trophic mass balance model of the eastern Chukchi Sea with comparisons to other high-latitude systems. Polar Biol 37:911-939

Wieczorek SK, Hooper RG (1995) Relationship between diet and food availability in the snow crab, *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. J Crustac Biol 15:236-247

Wooller MJ, Zazula GD, Edwards M, Froese DG, Boone RD, Parker C, Bennett B (2007) Stable carbon isotope composition of eastern Beringian grasses and sedges: investigating their potential as paleoenvironmental indicators. Arct Antarct Alp Res 39:318-331

Yasuda T (1967) Feeding habit of the Zuwaigani, *Chionoecetes opilio elongatus*, in Wakasa Bay. I. Specific composition of the stomach contents. Bull Jap Soc Sci Fish 33:315-319

Zheng, J, Kruse GH, Ackley DR (2001) Spatial distribution and recruitment patterns of snow crabs in the eastern Bering Sea. In: GH Kruse, N Bez, A Booth, MW Dorn, S Hills, RN Lipcius, D Pelletier, C Roy, SJ Smith, D Witherell (eds) Spatial processes and management of marine populations. AK-SG-01–02, Alaska Sea Grant, Fairbanks, 233-255

Table 2.1. Overall carapace width (CW) size ranges and number of stomachs analyzed for males, immature females, and mature females for each of the five study regions.

Region	Sex class	Size range (mm CW)	No. of Stomachs	No. isotope samples
southern Chukchi	males	40-80	78	79
southern Chukchi	immature females	40-50	24	26
southern Chukchi	mature females	30-60	NA	33
northern Chukchi	males	40-80	101	79
northern Chukchi	immature females	40-50	10	10
northern Chukchi	mature females	30-60	NA	32
western Beaufort	males	30-70	26	24
western Beaufort	immature females	30-50	5	5
western Beaufort	mature females	30-60	3	3
central Beaufort	males	50-120	64	33
central Beaufort	immature females	60-70	3	3
central Beaufort	mature females	60	2	2
Canadian Beaufort	males	80-130	22	28

Table 2.2. Ranked biomass and abundance prey taxa for five stations from the 2012 RUSALCA cruise and for five carapace width (CW) size classes of snow crabs collected at close-by stations to the 2012 Arctic EIS cruise to the southern Chukchi Sea (see Fig. 2.1 for station locations) "—" indicates that prey taxa were absent at a station.

Station	Polychaeta	Bivalvia	Crustacea	Sipuncula	Ophiuroidea	Echinoidea	Anthozoa	Ascidiacea	Nemertea	Others
Biomass (g C m^{-2})										
CS8R	3	1	2	7	4	—	6	—	8	5
CS12R	4	1	2	—	—	—	3	—	5	6
CS17	4	2	6	5	7	10	9	3	8	1
CL1	1	2	4	8	5	7	—	—	6	3
CL3R	2	3	4	1	6	7	—	—	—	5
Abundance (individuals m^{-2})										
CS8R	3	2	1	8	5	—	6	—	7	4
CS12R	3	2	1	—	—	—	4	—	6	5
CS17	1	6	2	5	3	9	—	7	8	4
CL1	2	1	3	7	4	6	—	—	—	5
CL3R	2	1	3	6	5	6	—	—	—	4
Snow Crab CW size class										
40 mm	3	1	2	—	4	—	—	—	—	5
50 mm	1	2	3	—	4	—	—	—	—	5
60 mm	2	1	3	—	5	—	—	—	—	4
70 mm	1	2	2	—	—	—	—	—	—	3
80 mm	1	2	3	—	—	—	—	—	—	—

Table 2.3. PERMANOVA results comparing diet composition among carapace width size classes (CW) and sex-age classes within study regions in the Chukchi and Beaufort Seas. Results shown indicate variance components explained by region, body size, and sex-age class for stomach contents analysis, as well as F-statistics and significance.

Source of variation	df	SS	MS	Pseudo-F	P (based on 999 permutations)
Stomach Contents Analysis- Region, CW, Sex-age as fixed variables					
Among regions	3	20333.0	6777.7	2.8	**0.001**
Among CW	9	27793.0	3088.2	1.3	0.056
Among Sex-age	1	1680.3	1680.3	0.7	0.718
Region*CW	13	42935.0	3302.7	1.4	**0.002**
Region*Sex-age	3	9085.7	3028.6	1.2	0.182
CW*Sex-age	4	10605.0	2651.2	1.1	0.344
Region*CW*Sex-age	2	3123.7	1561.9	0.6	0.874
Stomach Contents Analysis- post-hoc pairwise regions					
southern Chukchi- northern Chukchi					0.208
southern Chukchi- western Beaufort					0.281
southern Chukchi- central Beaufort					**0.001**
southern Chukchi- Canadian Beaufort					**0.025**
northern Chukchi- western Beaufort					0.338
northern Chukchi- central Beaufort					**0.001**
northern Chukchi- Canadian Beaufort					**0.008**
western Beaufort- central Beaufort					0.655
western Beaufort- Canadian Beaufort					**0.013**
central Beaufort- Canadian Beaufort					**0.001**
Stomach Contents Analysis- Individual region CW groups					
southern Chukchi	4	24572.0	6143.1	2.2	**0.001**
northern Chukchi	4	10109	2527.4	1.0	0.473
central Beaufort	7	21653.0	3093.3	1.7	**0.007**
western Beaufort	4	9717.5	2429.4	1.1	0.305
Canadian Beaufort	4	10150	2537.6	0.8	0.656

Table 2.4. PERMANOVA results comparing stable isotope analysis (SIA) among carapace width size classes (CW) and sex-age classes within study regions in the Chukchi and Beaufort Seas. Results shown indicate variance components explained by region, body size, and sex-age class,

as well as F-statistics and significance. Post-hoc comparisons are provided at the regional and the sex-age levels.

Source of variation	df	SS	MS	Pseudo-F	P (based on 999 permutations)
SIA-Region, CW, Sex-age as fixed variables					
Among regions	4	0.61	0.15	7.1	**0.001**
Among CW	9	0.13	0.01	0.7	0.722
Among Sex-age	2	0.15	0.10	4.7	**0.034**
Region*CW	14	0.25	0.02	0.8	0.654
Region*Sex-age	6	0.24	0.04	1.9	0.056
Region*CW*Sex-age	4	0.06	0.02	0.7	0.658
SIA- post-hoc pairwise regions					
southern Chukchi-northern Chukchi					0.064
southern Chukchi-western Beaufort					0.084
southern Chukchi-central Beaufort					**0.009**
southern Chukchi-Canadian Beaufort					**0.001**
northern Chukchi-western Beaufort					0.137
northern Chukchi-central Beaufort					0.073
northern Chukchi-Canadian Beaufort					**0.002**
western Beaufort-central Beaufort					**0.002**
western Beaufort-Canadian Beaufort					**0.013**
central Beaufort-Canadian Beaufort					**0.001**
SIA-post-hoc pairwise within region					
southern Chukchi					
male-immature female					**0.001**
male-mature female					**0.005**
immature female-mature female					0.981
northern Chukchi					
male-immature female					0.848
male-mature female					0.547
immature female-mature female					0.724
western Beaufort					
male-immature female					0.140
male-mature female					0.055
immature female-mature female					0.056
central Beaufort					
male-immature female					0.937
male-mature female					0.064
immature female-mature female					0.094

Table 2.5. Mann-Whitney U-tests comparing ranked prey biomass and abundance *in situ* to ranked importance (based on frequency of occurrence [%]) of snow crabs within the southern Chukchi Sea.

Source of variation	df	U	P-value
Polychaeta (biomass)	1	2.32	0.13
Polychaeta (abundance)	1	1.22	0.27
Bivalvia (biomass)	1	0.12	0.73
Bivalvia (abundance)	1	0.12	0.73
Crustacea (biomass)	1	0.97	0.32
Crustacea (abundance)	1	1.04	0.31
Ophiuroidea (biomass)	1	0.05	0.83
Ophiuroidea (abundance)	1	0.29	0.59
Echinoidea (biomass)	1	3.75	0.05
Echinoidea (abundance)	1	3.75	0.53
Anthozoa (biomass)	1	3.71	0.05
Anthozoa (abundance)	1	2.22	0.14
Ascidiacea (biomass)	1	1.00	0.32
Ascidacea (abundance)	1	1.00	0.32
Sipuncula (biomass)	1	5.53	**0.02**
Sipuncula (abundance)	1	5.54	**0.02**
Nemertea (biomass)	1	5.58	**0.02**
Nemertea (abundance)	1	3.72	0.05
Other prey (biomass)	1	0.20	0.67
Other prey (abundance)	1	0.20	0.66

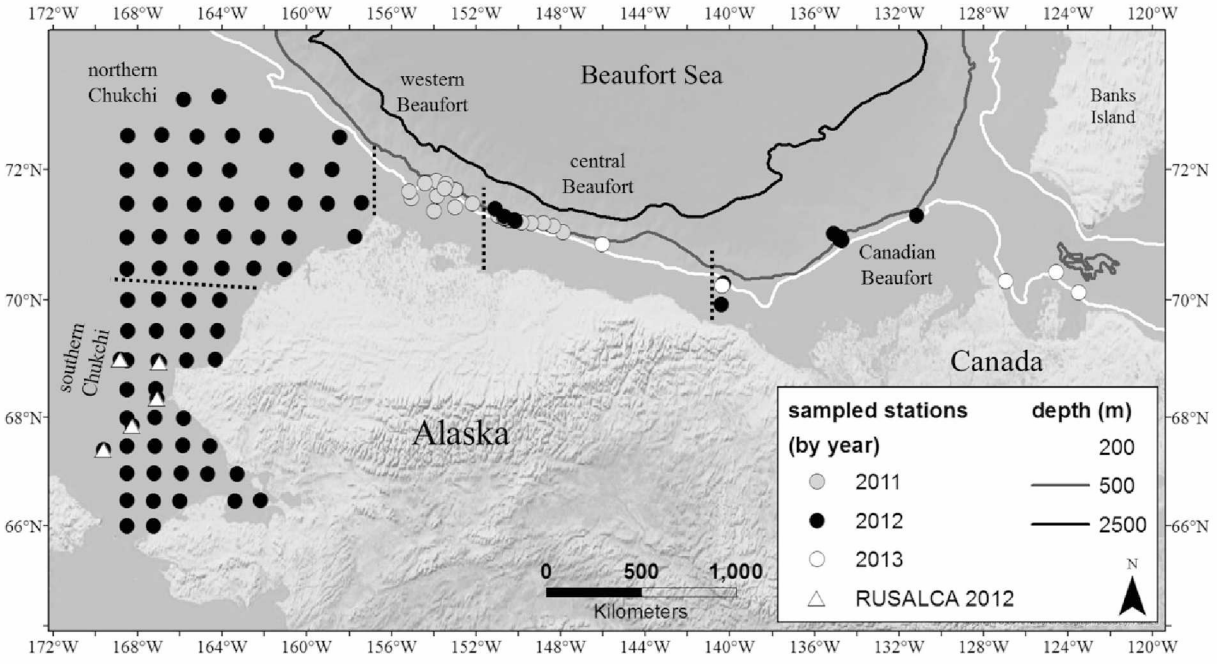

Figure 2.1. Map of station locations in the Chukchi and Beaufort seas where snow crab collections occurred. Stations are shaded by year of collections. White triangles represent RUSALCA stations where macrofauna were collected for prey availability analysis. Regions are delineated by black dotted lines.

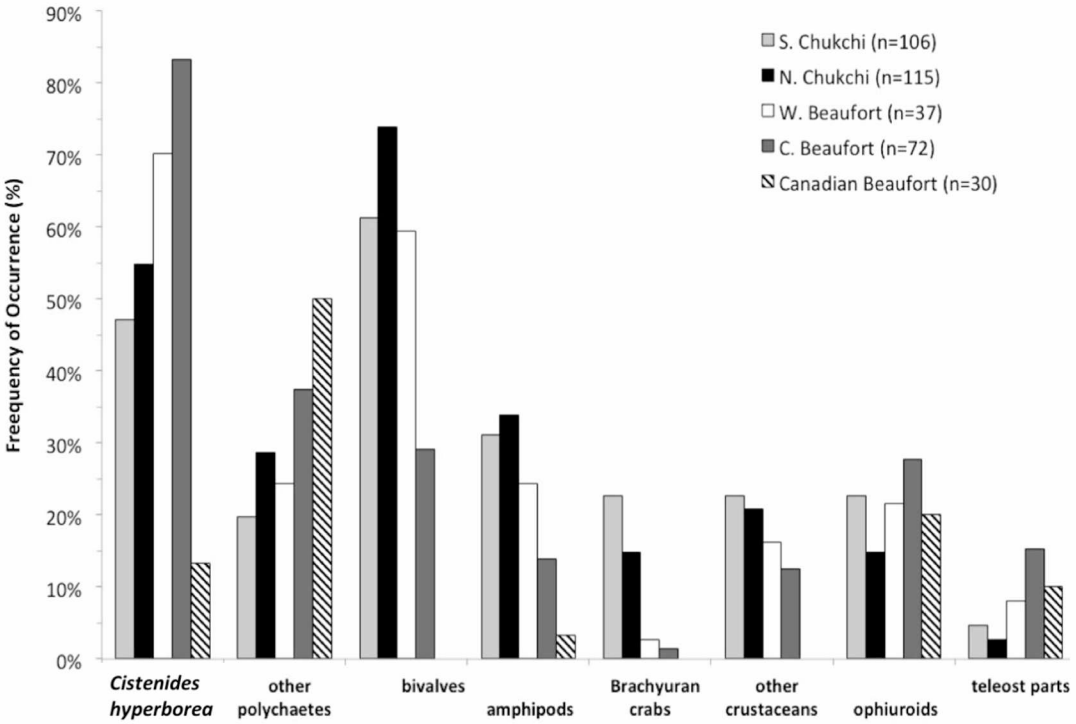

Figure 2.2. Frequency of occurrence (%) data for the most common prey taxa categories by regions in the Chukchi and Beaufort Seas. Sample sizes for each region are indicated in parentheses in the legend.

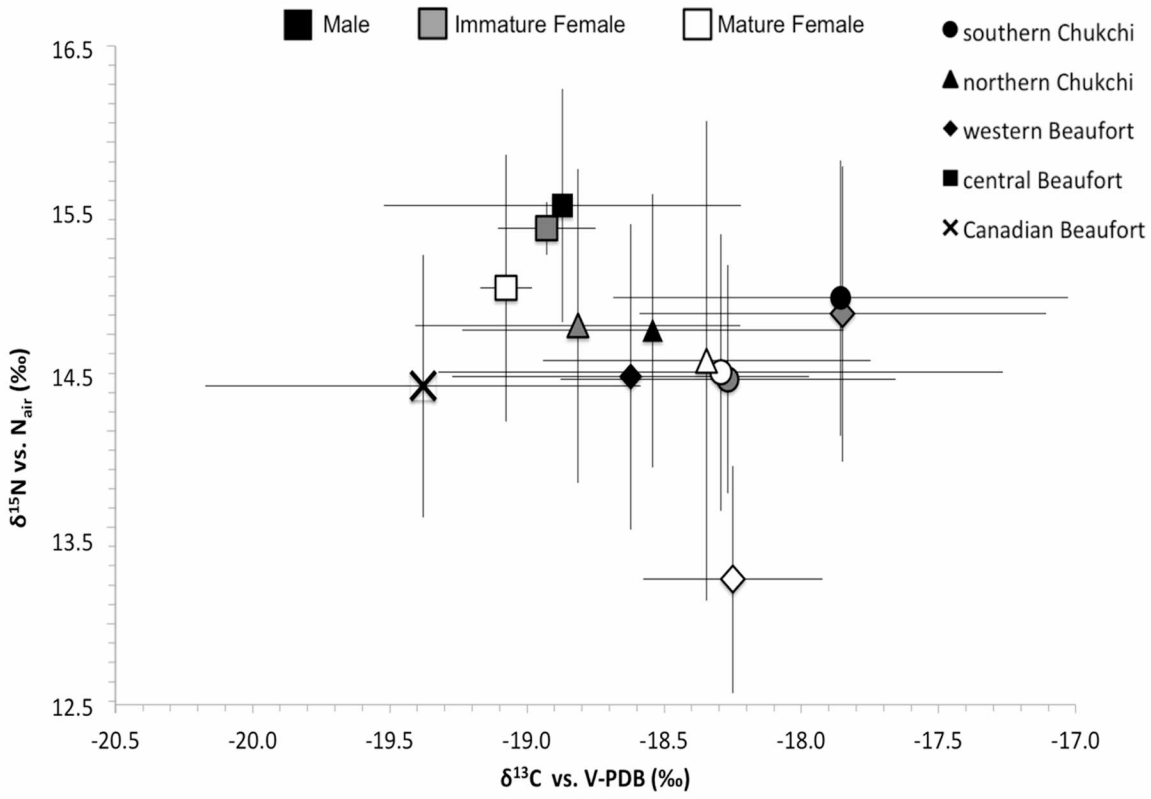

Figure 2.3. Mean $\delta^{13}C$ and $\delta^{15}N$ stable isotope values for males and immature and mature females for five regions: southern and northern Chukchi Sea and western, central, and Canadian Beaufort Sea. Error bars are ±1 S.D.

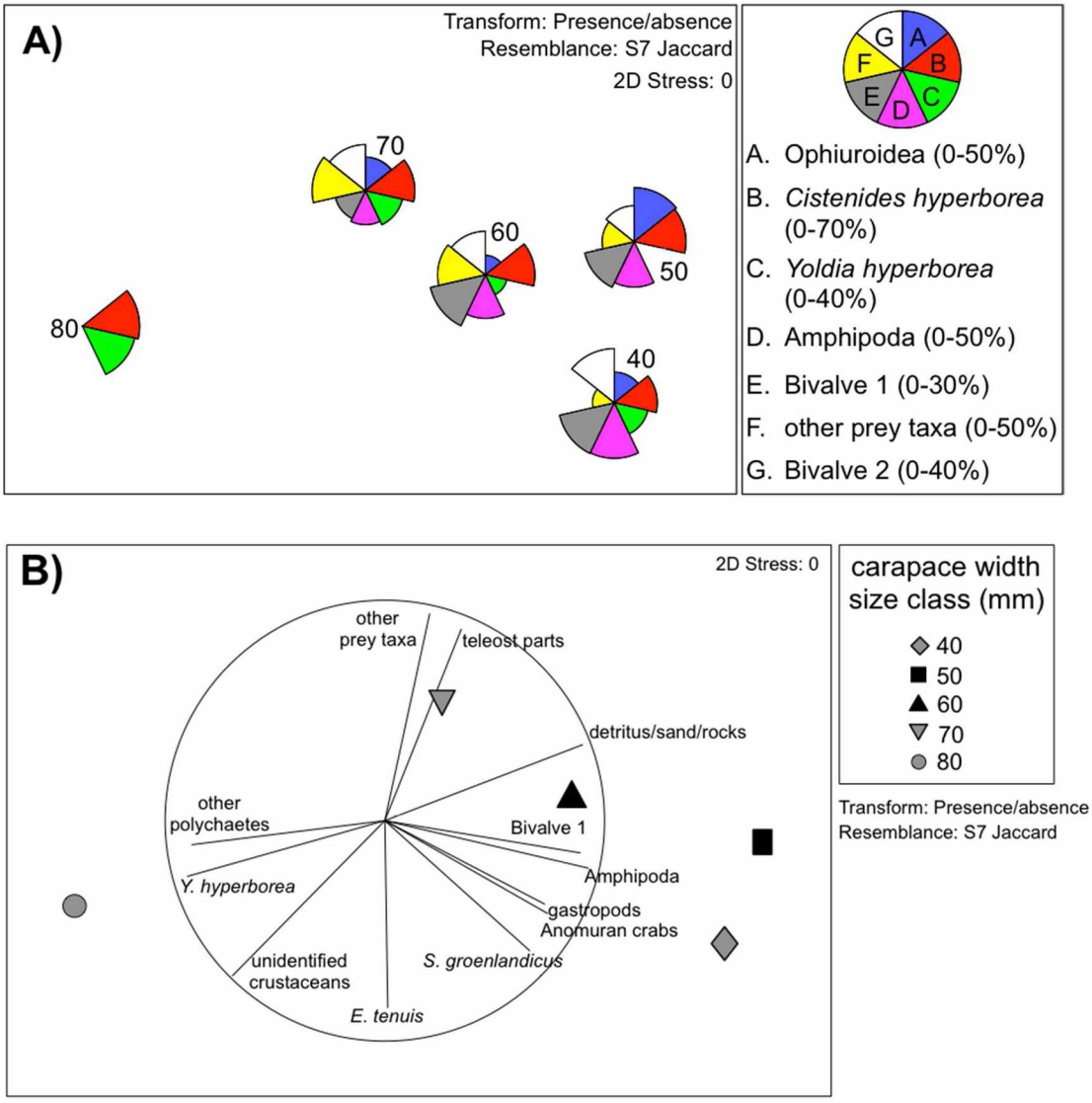

Figure 2.4. MDS plots for snow crabs in the southern Chukchi Sea showing A) seven prey taxa contributing to differences among size classes (carapace width size classes are represented numerically) and their frequency of occurrence (FO) within diets for each size class (FO minimum to maximum range indicated in parentheses). Pie pieces are proportional within each specified taxa to the range of FO occurring among size classes. B) Prey taxa that contributed to dissimilarities in the diets among various carapace width size classes as indicated in SIMPER analysis. Distances among data points are proportional to the degree of dissimilarity among size classes and overlaid directional lines indicate prey taxa that contribute to these dissimilarities.

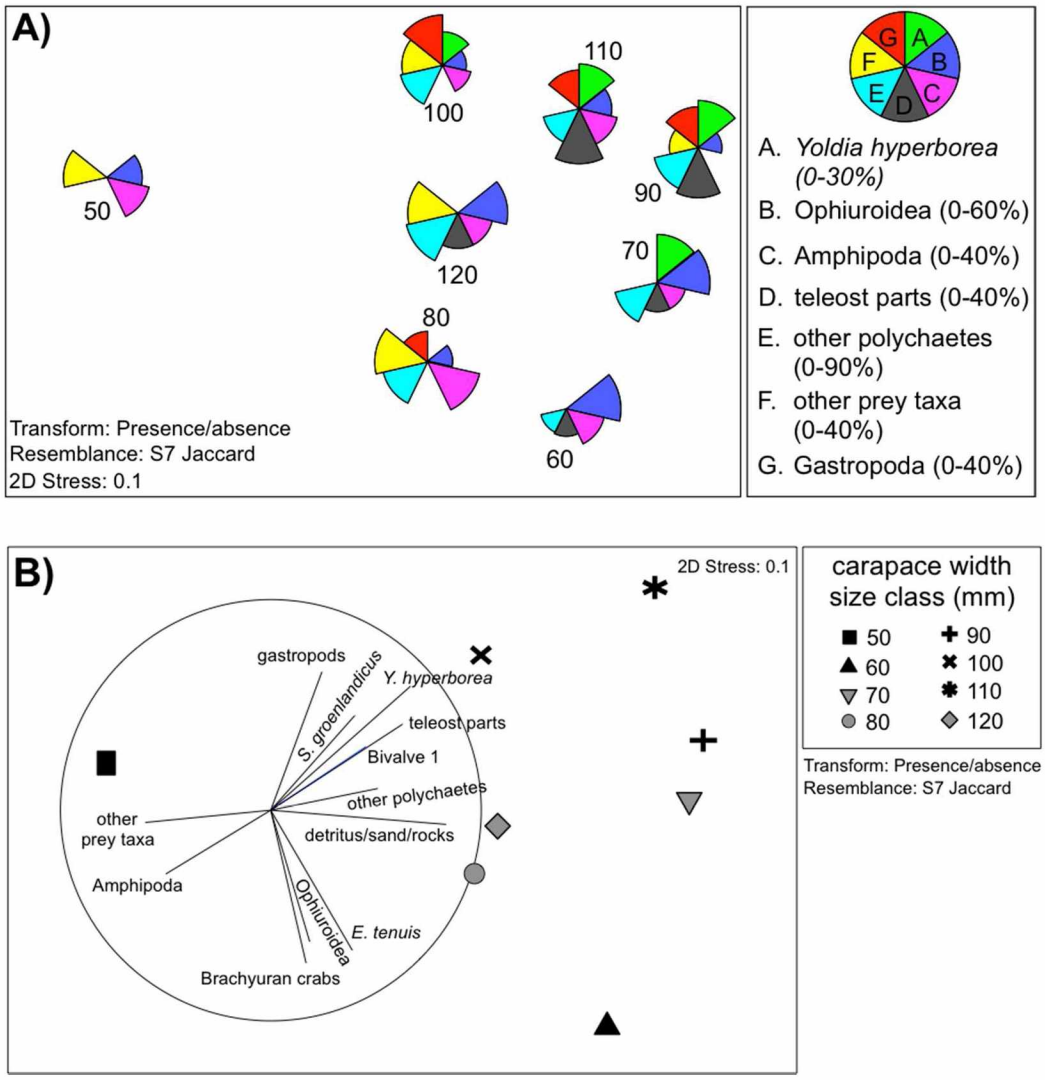

Figure 2.5. MDS plots for snow crabs in the central Beaufort Sea showing A) seven prey taxa contributing to differences among size classes (carapace width size classes are represented numerically) and their frequency of occurrence (FO) within diets for each size class (FO minimum to maximum range indicated in parentheses). Pie pieces of each specified taxa are proportional to the range of FO occurring among size classes. B) Prey taxa that contributed to dissimilarities in the diets among various carapace width size classes as indicated in SIMPER analysis. Distances among data points are proportional to the degree of dissimilarity among size classes and overlaid directional lines indicate prey taxa that contribute to these dissimilarities.

CHAPTER 3

New estimates of biomass, abundance, maximum sustainable yield, length-weight relationships, size-at-maturity, and fecundity of snow crab, *Chionoecetes opilio*, in the Arctic Ocean off Alaska[3]

Abstract

Snow crabs (*Chionoecetes opilio*) were identified as a potential future target fisheries species in the Fishery Management Plan for the Fish Resources of the Arctic Management Area (Arctic FMP) in 2009, but a moratorium currently prohibits commercial fishing in federal waters of the Arctic Ocean off Alaska. One problem of the current Arctic FMP is the limited data on which critical snow crab population and biomass estimates are based. Collaborative research efforts in the Chukchi and Beaufort seas over the past decade have yielded a much richer database on Arctic snow crabs. Here, we generated new estimates of stock biomass and abundance to re-calculate sustainable yield of snow crab in the Alaskan Arctic, as well as length-weight relationships, size-at-maturity, and female fecundity. Although snow crabs were more abundant in the Chukchi Sea, harvestable biomass of male snow crabs only occurred in the Beaufort Sea because no crabs larger than the minimum marketable size (≥ 100 mm carapace width, based on Bering Sea metric) occurred in the Chukchi Sea during the study period. Our estimates for biomass and sustainable yield in the Beaufort Sea are lower than previous estimates

[3] In preparation for publication: Divine LM, Mueter FJ, Kruse GH, Bluhm BA, Iken K. New estimates of biomass, abundance, maximum sustainable yield, length-weight relationships, size-at-maturity, and fecundity of snow crab, *Chionoecetes opilio*, in the Arctic Ocean off Alaska. Prepared for: Canadian Journal of Fisheries and Aquatic Sciences.

in the Arctic FMP. Length-weight relationships were generally similar for male and female snow crabs between the Chukchi and Beaufort seas. Size-at-maturity was slightly smaller, and fecundity was similar at a given size, for Chukchi Sea female snow crabs than for snow crabs occurring in other geographic regions; low sample sizes in the Beaufort Sea prevented size-at-maturity and fecundity analyses. Our results expand overall understanding of Arctic snow crab dynamics and inform management of the snow crabs in the Alaskan Arctic in light of potential future fisheries and other, non-fishing activities.

Key words: Fishery Management Plan for the Fish Resources of the Arctic Management Area (Arctic FMP), Beaufort Sea, Chukchi Sea, sustainable yield

Introduction

Snow crab *Chionoecetes opilio* are widely distributed across sub-Arctic and Arctic waters, with lucrative commercial fisheries occurring in the North Atlantic (eastern Canada and Greenland), Bering Sea, and Sea of Japan. Although minimum legal size is 78 mm carapace width (CW), minimum marketable size in the Bering Sea is 100 mm CW; thus, harvest is limited to only males $\geq$ 100 mm CW in an attempt to protect female reproductive potential (Zheng and Kruse 2006, Turnock and Rugolo 2012). In 1999, the eastern Bering Sea (EBS) fishery was declared overfished after a period of declining snow crab biomass and abundance (Turnock and Rugolo 2012). Additionally, a northward contraction of the center of snow crab distribution in the EBS in response to changing oceanographic conditions was identified shortly after overfishing was recognized (Zheng et al. 2001, Orensanz et al. 2004). The combination of the biomass decline, a distribution shift in the EBS snow crab stock, and high abundances of snow

crabs in the northern Bering Sea (NPFMC 2009, Kolts et al. 2015), have raised concerns about the possibility of this species moving further out of EBS fishing grounds and northward into Arctic waters. In response to a potential future fishery in the Alaskan Arctic, the Fishery Management Plan for the Fish Resources of the Arctic Management Area (Arctic FMP) was developed by the North Pacific Fishery Management Council (NPFMC 2009). Authors of the Arctic FMP had to rely on limited available Arctic snow crab population data and applied life history metrics estimated from snow crab populations from other regions to evaluate total and harvestable biomass in the Chukchi and Beaufort seas.

Exploitable snow crab biomass is currently presumed to be low in the Alaskan Arctic, although snow crabs are dominant members of benthic communities with respect to biomass and abundance in the Chukchi Sea and in the western Beaufort Sea (Bluhm et al. 2009, Rand and Logerwell 2011, Ravelo et al. 2014, 2015). The potential commercial exploitation of Arctic snow crab requires detailed knowledge of their stock structure and life history in the Arctic. However, snow crab populations in the Chukchi and Beaufort seas have not been historically monitored with any regularity due to the lack of federal monitoring programs and challenges of sampling the vast, seasonally ice-covered shelves and slopes. In the Chukchi Sea, snow crabs contribute significantly to overall invertebrate biomass, even at small body sizes (i.e., 74 mm CW, Frost and Lowry 1983, Paul et al. 1997; 94 mm CW, Gross 2015). Limited available data suggest that snow crab abundance has increased on the Chukchi shelf by at least an order of magnitude over the last few decades (Feder et al. 2005) although individual snow crab body sizes remain small. Abundance estimates in the Beaufort Sea have increased because recent deeper sampling yielded more and larger crabs than on the shelf (Logerwell and Rand 2010, Bluhm et al. 2015) and the maximum size of snow crabs collected in the Beaufort Sea has increased from 75 mm carapace

width (CW) recorded in the 1970s (Frost and Lowry 1983) to 119 mm CW in the 2000s (Rand and Logerwell 2011). Thus, marketable-sized crabs occur in the Beaufort Sea, either as a new development since the 1970s or due to more intense and deeper sampling efforts in the 2000s.

A clear understanding of life history, maturation processes, population structure, and fecundity is essential for effective management of snow crab stocks (Comeau and Conan 1992, Sainte-Marie et al. 1995), including the development of sustainable harvest limits (NPFMC 2009). Snow crab life history and growth has been best studied in geographic regions where snow crabs are commercially exploited (e.g., Gulf of St. Lawrence: Watson 1970, Haynes et al. 1976, Comeau and Conan 1992, Sainte-Marie et al. 1995, Comeau et al. 1998; Bering Sea: Haynes et al. 1976, Otto 1998, Orensanz et al. 2007, Ernst et al. 2012). Snow crabs undergo a series of molts during which they exhibit discrete increases in body size (Hartnoll 1982). Somatic growth for males and females is similar at small sizes (i.e., 3-10 mm CW, corresponding to ages 0^+ to 4 years, Comeau et al. 1998), but males molt more frequently and molt increments are larger at later stages, resulting in larger maximum sizes for males relative to females (Alunno-Bruscia and Sainte-Marie 1998, Burmeister and Sainte-Marie 2010, Dawe et al. 2012). Males and females undergo a final, terminal molt to maturity at an estimated age of 7+ years after settlement (for Canadian Atlantic regions), but size at terminal molt is highly variable among individuals and sexes (Conan and Comeau 1986, Comeau and Conan 1992, Comeau et al. 1998, Sainte-Marie et al. 1995, 2008, Burmeister and Sainte-Marie 2010). In cold waters (< 0°C) snow crabs exhibit slower growth rates, have a smaller growth increment per molt, or skip a molt, all of which can result in smaller terminal sizes (Burmeister and Sainte-Marie 2010, Dawe et al. 2012). Skip-molting is more common in later instars, shortly before the terminal molt to maturity, and especially females at low temperatures may be forced to skip-molt if they do not

reach the physiological threshold to accomplish the energetically costly female terminal molt (Dawe et al. 2012). Males, in turn, may skip-molt late in their adolescent development to eventually reach larger terminal sizes, which will increase their life-time fitness (Sainte-Marie et al. 2008, Dawe et al. 2012). All of this complicates the application of growth models to Arctic snow crab populations.

Size-at-maturity is a critical determinant of reproductive output and rate of population growth in brachyuran crabs (Stearns 1976, Hines 1982). Male crabs exhibit an allometric increase in chela height relative to body size during the terminal molt (Conan and Comeau 1986), and this relationship is used to determine maturity status for males. However, gonad development occurs prior to terminal molt and males may be sexually mature prior to exhibiting a change in chela allometry (Sainte-Marie et al. 1995). For example, males in the Gulf of St. Lawrence reach 50% physiological maturity at 34 mm CW based on presence of spermatophores inside the vas deferens (Comeau and Conan 1992), but reach 50% morphometric maturity at 57 mm CW based on chela allometry (Watson 1970). Moreover, size-at-maturity varies with latitude. For instance, based on chela allometry males mature at a minimum of 65 mm CW in the eastern Bering Sea (Somerton 1981), compared with minimum sizes of ~ 40 mm CW in the Chukchi Sea (Barber et al. 1994). For females, maturity is indicated by a marked increase in the size of the abdominal flap to accommodate an egg clutch after their terminal molt (Watson 1970, Moriyasu et al. 1987, Alunno-Bruscia and Sainte-Marie 1998). Temperature dependence of size-at-maturity may be reflected in a latitudinal trend, where size-at-maturity in female snow crabs based on abdominal flap size decreases from 60-67 mm CW in the southeastern Bering Sea to 50-52 mm CW in the northern Bering Sea (Somerton 1981, Otto 1998, Ernst et al. 2005, Armstrong et al. 2008) but then remains similar around 50 mm CW in the northern Chukchi Sea

in 1976 (Jewett 1981). However, the mean CW at 50% maturity of females collected during 1990-1991 (Paul et al. 1997) and in the 2000s (Bluhm et al. 2015) in the Chukchi Sea was smaller, estimated at 46 mm. In general, though, while size-at-maturity is strongly temperature-driven, it does typically occur over a range of sizes within a geographic region (Dawe et al. 2012).

Female fecundity (i.e., number of fertilized eggs per clutch) and female lifetime fecundity (i.e., number of eggs produced in a lifetime) are important metrics in understanding distribution patterns in crab stocks and their changes over time (Armstrong et al. 2008). In the Bering Sea, female fecundity is scaled to body size, with larger females producing larger egg clutches (Orensanz et al. 2007, Kolts et al. 2015). In response to cold ($\leq$ ~1 °C) annual mean temperatures in the northern Bering Sea, females shift from an annual to a biennial breeding cycle (Rugolo et al. 2005, Kolts et al. 2015). For the Alaskan Arctic, it is unclear whether mature females breed annually or biennially and, if biennial breeding occurs, what proportion of mature females are on a biennial breeding schedule. Virtually no mature females with fertilized egg clutches have been collected in the Beaufort Sea to date (Bluhm et al. 2015), indicating zero to minimal local reproduction in this region.

The goal of the present study was to provide new information on high Arctic snow crab life history and distribution in the Chukchi and Beaufort seas, using a synthesis of available data collected over the past decade. Specifically, we estimated (1) regional biomass, abundance, and sustainable yield for snow crabs in the Chukchi and Beaufort seas, (2) individual length-weight relationships for snow crabs in the Chukchi and Beaufort seas, (3) size-at-maturity for males and females in the Chukchi Sea only, and (4) fecundity of females in the Chukchi Sea only, due to

low sample sizes in the Beaufort Sea. We used these data to revise total and harvestable biomass estimates originally published for snow crabs in the Arctic FMP (NPFMC 2009).

2. Methods

2.1 Snow crab collections

This project used a combination of snow crab data collected from 19 surveys, 12 in the Chukchi Sea and 7 in the Beaufort Sea between 2004 and 2015 (Table 3.1, Fig. 3.1). New samples and/or existing data were used in various combinations to address project objectives (e.g., subsets of data were used for various calculations and analyses as appropriate). A vast majority of crabs were collected with a plumb staff beam trawl (PSBT, modified from Gunderson and Ellis 1986, see details on towing methods in Norcross et al. 2015; Table 3.1). The PSBT has an effective 2.26 m opening and a net with square mesh of 7 mm and a 4 mm cod end liner. Tow duration lasted from 1-6 min at speeds ranging 1-1.5 kts. Crabs were also collected using an 83-112 Nor'Eastern bottom trawl (EBT, Table 3.1), which is the standard net for the Alaska Fisheries Science Center (AFSC) bottom trawl surveys in the EBS. The EBT has a 25.3 m headrope and 34.1 m footrope. During the Ocean Explorer survey in the Beaufort Sea in 2008 and the Arctic Ecosystem Integrated Survey (Arctic Eis) 2012 survey (Table 3.1), the EBT was fitted with a net mesh of 102 mm, with 89 mm intermediate and cod end liners (see Rand and Logerwell 2011 for information on lined or unlined tows during 2008 Ocean Explorer cruise). During the Arctic Eis cruise, the cod end had a 32 mm liner (Goddard et al. 2012). Tow duration for the EBT ranged from 5 to 15 min at an approximate speed of 3 kts.

To correct for gear bias in the size composition estimate of the snow crab population in the Chukchi Sea, we compared the size frequencies of crabs between the PSBT and EBT based

on snow crab CW data from 33 paired trawls taken during the Arctic Eis 2012 cruise (Britt et al. 2013, Table 3.1). The observed size composition was summarized by gear type as the number of crabs per km^2 in each 1 mm size bin. The effectiveness of the two nets for sampling snow crabs in their path is unknown (catchability) and is likely to differ among crab sizes (size selectivity). Assuming each trawl is fully size selective (selectivity = 1) over some range of observed sizes (CW), the size selectivity of the two trawl types can be estimated under the following assumptions. We first used the common assumption that selectivity follows a logistic model of the form:

$$\text{selectivity} = \frac{1}{1+e^{b(x-a)}},$$

where x is the carapace width, parameter a corresponds to size at 50% selectivity, and b corresponds to the steepness of the curve. We further assumed that selectivity of the EBT approaches 1 for large crabs (large mesh size) and selectivity may decrease with decreasing CW ($b > 0$), whereas the PSBT has full selectivity for small snow crabs (small mesh size) and selectivity may decrease with increasing CW ($b < 0$).

We simultaneously estimated the parameters of the two selectivity curves by minimizing a weighted sum of squared differences between the predicted number of crabs at size k from the PSBT and the predicted number of crabs at size k from the EBT. Because the variability in numbers at size was not constant and increased with the number of crabs (N_k) in size bin k, we applied appropriate weights to the squared differences before summing across size bins. We assumed that variance increases linearly with N_k based on the expected mean-variance relationship for Poisson-distributed count data. We then weighted the squared difference for each size bin by $1/N_k$, where N_k values were computed from a smoothed length-frequency distribution that was estimated by minimizing the unweighted sum of squares. If the number of crabs in a

given size bin was estimated to be less than 1 it was set equal to 1 to avoid assigning excessive weights to these bins. This selectivity analysis was used to determine a size range over which both gears had similar high selectivity to pool snow crab abundances and biomass across gear types. Estimated size selectivity was used to estimate the "true" size distribution of crabs in the Chukchi Sea by dividing the observed numbers at a given size by the estimated selectivity at that size. The methods used in the present study differ from previous biomass estimates in the Arctic FMP in that the Arctic FMP used only data collected with the EBT that were not corrected for selectivity (NPFMC 2009).

Snow crabs collected from all trawls were rinsed and counted, bulk weight per station recorded using spring or digital hanging scales, and during some cruises, carapace width (body size) was measured to the nearest 0.1 mm using digital Vernier calipers. Crabs were either frozen whole or preserved in formalin (RUSALCA 2009 only) for transport to the laboratory. Crabs were then thawed, blotted dry, and individually weighed to the nearest 0.1 g. When necessary, crabs with missing limbs were weighed with remaining limbs attached; then limbs were removed where missing legs occurred on the opposite side, these limbs weighed and added to the body weight for a total individual weight.

2.2 Biomass, abundance, and sustainable yield

Biomass and abundance at each station were standardized based on the area swept by the trawl. For the EBT, area swept was determined by multiplying the distance towed by the mean net spread. For the PSBT, the net width was assumed to be fixed at 2.257 m (Gunderson and Ellis 1986), and area swept was equal to the net width multiplied by the distance towed. Catches were standardized by computing catch per unit effort (CPUE) in numbers or biomass (kg) per km^2. Because sampling locations differed among years we assumed that abundances did not

change over the study period and aggregated all samples in 1° latitude x 1° longitude grid cells in the Chukchi Sea (for a total of 44 grid cells, Fig. 3.1). We then averaged CPUE across all samples within a grid cell, multiplied mean CPUE by the area of the grid cell to obtain an estimate of biomass or abundance per grid cell, and finally summed over all grid cells to estimate total region-wide biomass or abundance over the total survey area in the US Chukchi Sea (145,200 km^2). Total survey area was bounded by the outer periphery of all sampled stations (MATLAB, V. 7.10.0 Natick, MA, Fig. 3.1). In the Beaufort Sea, which has a narrow shelf and a steeper depth gradient, we divided the survey area into two depth strata: shallow stations < 100 m depth, and deep stations > 100 m depth. Total biomass and abundance of snow crab in each depth stratum was computed as for grid cells in the Chukchi Sea and was summed over the two depth strata to estimate abundance or biomass within the total survey area of 65,002 km^2. While this alleviated some potential biases due to uneven sampling, these estimates are making the strong assumption that samples within each stratum were independent, random samples.

Estimates obtained here were considered pristine, or unfished, biomass for comparison with previous estimates from the Arctic FMP (NPFMC 2009). For the comparison, we determined the equilibrium biomass following Thompson (1992) as:

$$B(F|r) = \left[\left(\frac{h}{M+F}\right)\left(1+\frac{1}{(M+F)d}\right)\right]^{\frac{1}{r}},$$

where F is the instantaneous fishing mortality, r is the amount of resilience implied by the stock recruitment relationship, h is the scale parameter in Cushing's (1971) stock-recruitment relationship, M is the instantaneous natural mortality rate, and d is the difference between the age-at-maturity and the age intercept of the linear weight-at-age equation (Thompson 1992, NPFMC 2009). As this stock has not been historically fished, we set $F = 0$. To determine the amount of biomass available to future potential fishing harvest based on our new biomass

estimates, we determined sustainable yield as the product of F and equilibrium biomass:

$$Y(F|r) = F \cdot B(F|r).$$

We then obtained an estimate of the instantaneous fishing mortality that maximizes sustainable yield as:

$$F_{MSY}(r) = \left(\frac{M}{2(1-r)}\right)\left(1 - \frac{2-r}{M*d} + \sqrt{\left(\frac{(2-r)}{M*d}\right)^2 + \frac{4-6r}{M*d} + 1}\right) - M.$$

The biomass at which a maximum sustainable yield (MSY) can be obtained was calculated as:

$$B_{MSY} = B\mathit{ratio}(F_{MSY}(r)|r) \cdot B_0,$$

where B*ratio* is the ratio of equilibrium biomass to unfished (pristine) biomass (B_0). Finally, the maximum sustainable yield was estimated as:

$$MSY = Y\mathit{ratio}(F_{MSY}(r)|r) \cdot B_0,$$

where Y*ratio* is the ratio of sustainable yield (Y(F|r)) to B_0. We compared our estimates of unfished and equilibrium biomass and maximum sustainable yield to values put forth in the Arctic FMP (NPFMC 2009).

2.3 Length-weight relationships

To quantify snow crab length-weight relationships, we fit a linear regression of log-transformed wet body mass (M in g) on size (CW in mm) as follows:

$$\log M = a_{sk} + b_{sk} \cdot \log CW,$$

where M = mass, a is the intercept, and b is the slope, which may vary between sexes (s) and between the Chukchi and Beaufort Sea (k). Analysis of covariance (ANCOVA) was performed to determine if the size relationships differed significantly between the Chukchi and Beaufort seas for immature and mature males and females. Females were separated into immature and mature status because mature female growth is disproportionately allocated to reproduction rather than somatic growth (Alunno-Bruscia and Sainte-Marie 1998), and female maturity was

determined morphometrically during all cruises used in the present study. Males were divided into mature males and juvenile/ adolescent males by using a dividing line of CH = 0.191 · CW to determine maturity (Kolts et al. 2013; see size-at-maturity methods below).

Size frequency distributions (SFD) were established at 1 mm CW increments separately for the Chukchi and Beaufort seas from all size data available, and pooled across years, to characterize the size ranges of male and female crabs. Assuming that these pooled data are representative of the population, we attempted a mixed modal analysis for observed SFD histograms to identify modal peaks that may be interpreted as instars or ages (Kolts et al. 2015). Unfortunately, clear peaks in the size frequency distributions did not occur and precluded our ability to make estimates of numbers-at-age. This may be due to temporal variability and/ or because skip-molting causes some bias in size-at-age relationships in cold water environments (Dawe et al. 2012).

2.4 Size-at-maturity

For male snow crabs from the Chukchi Sea, size-at-maturity was determined based on a relationship between the proportion of males exhibiting large rather than small chela relative to body size (Conan and Comeau 1986). Sample sizes were too low to determine size-at-maturity for either sex in the Beaufort Sea. To determine a breakpoint in the allometric relationship for male size-at-maturity estimates, observed male CW and chela height (CH) were plotted against several published regression equations (i.e., from the Bering Sea, Kolts et al. 2013 and Newfoundland, Comeau et al. 1998, data not shown here) to determine the existing relationship that best fit our data based on a visual assessment. The northern Bering Sea data presented the best fit for male snow crab data in the Chukchi Sea; thus, mature males were distinguished from juvenile and adolescent males by using a dividing line of CH = 0.191 ·CW (Kolts et al. 2013).

Female maturity was determined as the carapace width at which the abdominal flap covers the entire ventral side of mature females (Paul et al. 1997), as well as those visibly carrying an egg clutch. This was done for the Chukchi Sea only, as very few mature females were recovered from the Beaufort Sea during the study period. Size-at-maturity was determined by fitting logistic curves to males and females separately to obtain a maximum likelihood estimate of the proportion of mature crabs by size and sex.

2.5 Fecundity

Fecundity was estimated as the number of eggs per clutch taken from 306 mature females collected at random during the 2009 and 2012 RUSALCA, 2010 COMIDA, 2010 CSESP, and 2012 Arctic Eis cruises in the Chukchi Sea. 'Egg clutch' refers to the total number of fertilized eggs, or embryos, being carried by a female. Total egg clutch was removed from the pleopods, 250 eggs were sub-sampled, dried at 60 °C to a constant weight, and the dry weight of the sub-sample was determined (Stichert 2009). Remaining eggs were also dried as described above and total dry weight obtained. Fecundity was determined by dividing the weight of the total egg mass by the average dry weight of the eggs in the sub-sample and multiplying by the number of eggs in the sub-sample (250). A linear regression of the logarithm (log) of the total number of eggs on log-transformed carapace width was fit to the data to estimate the number of eggs in a clutch (dependent variable) as a function of body size (CW, independent variable). We did not attempt to characterize the developmental stage of eggs to judge whether reproduction was annual or biennial (see Kolts et al. 2015). However, data from Atlantic Canada, Greenland, and the nearby northern Bering Sea suggest that breeding is likely biennial over much of our study area (Moriyasu and Lanteigne 1998, Burmeister 2002, Kolts et al. 2015).

3. Results

3.1 Biomass, abundance, and sustainable yield

Our estimates of total (pristine) snow crab biomass in the Beaufort Sea survey area were approximately four times that of Chukchi total biomass (B_0 = 15,656 mt and 3,461 mt, respectively, Table 3.2). We estimated pristine harvestable biomass (males ≥ 100 mm CW) in the Beaufort Sea as B(F|r) = 1,722 mt. With an pristine harvestable biomass of 1,722 mt, and holding all other Arctic FMP parameters constant at the values used in the Arctic FMP (M= 0.23, d= 8.00, and F= 0.36), we estimated maximum sustainable yield in the Beaufort Sea to be MSY = 97mt with a biomass at maximum sustainable yield of B_{MSY} = 272 mt (Table 3.2). We did not estimate MSY or B_{MSY} for the Chukchi Sea because no males ≥100 mm CW occurred. We estimated a mean density of 387,691 individuals km^{-2} in the Chukchi Sea with an estimated total abundance of 56,292,775,896 individuals for the entire Chukchi Sea survey area. Abundance was much lower in the Beaufort Sea, with an estimated 47 individuals km^{-2}, and a total of 3,055,863 individuals for the entire survey region.

3.2 Size composition and length-weight relationships

Both trawl gears had similar size selectivity for snow crabs ≥ 41 mm CW. The PSBT had higher selectivity for crabs 30 mm to 42 mm CW (selectivity = 1.0 compared with selectivity 0.5 – 1.0 for EBT, Fig. 3.2, Table 3.3). The EBT had a selectivity of 0.4 for crabs 30 mm CW, but quickly increased and reached a selectivity of 0.5 by 32 mm CW, with selectivity approaching 1.0 for sizes ≥ 41 mm CW.

A total of 4,733 male and immature and mature female snow crabs ≥ 30 mm CW were individually measured and/or weighed across the Chukchi and Beaufort seas between 2004 and 2015 (Fig. 3.3 and 3.4). Although males were overall much less abundant in the Beaufort Sea

than in the Chukchi Sea, Beaufort males reached larger sizes (up to 120 mm CW, Fig. 3.3B), approximately 27 mm larger than the largest male collected in the Chukchi Sea (93 mm CW, Fig. 3.3A). Mature female snow crabs were also considerably less abundant in the Beaufort Sea compared with the Chukchi Sea, but also reached larger maximum sizes (82 and 72 mm CW in the Beaufort and Chukchi seas, respectively, Fig. 3.4B). Immature females in the Chukchi Sea ranged from 4 to 58 mm CW and mature females ranged from 21 to 72 mm CW (overlapping by 37 mm CW, Fig. 3.4A). In the Beaufort Sea, immature females ranged from 16 to 70 mm CW and mature females ranged from 37 to 82 mm CW (overlapping by 33 mm CW, Fig. 3.4B).

Length-weight relationships were similar between the Chukchi and Beaufort seas for immature and mature males (ANCOVA, $p= 0.72$ for both, Fig. 3.5). Length-weight relationships also were similar among immature and mature females between the Chukchi and Beaufort seas (ANCOVA, $p= 0.63$ for both, Fig. 3.6). However, females in the Chukchi Sea were heavier at a given CW than Beaufort Sea females (ANCOVA, $p< 0.0001$ for both immature and mature females). When considering immature versus mature female length-weight relationships within each region, we found contrasting patterns. Mature females in the Chukchi Sea achieved heavier body masses at a given size than immature females of the same size (ANCOVA, $p< 0.0001$, Fig. 3.6A and C), but the opposite pattern occurred in the Beaufort (ANCOVA, $p< 0.001$, Fig. 3.6B and D), where immature females were heavier at a given size than mature females. However, low sample sizes in the Beaufort Sea require cautious interpretation of the biological significance of this finding.

3.3 Size-at-maturity

For Chukchi Sea crabs, we estimated that 50% of male snow crabs reach reproductive maturity at 62 mm CW, based on morphometric allometry with chela height (Fig. 3.7A). Female

snow crabs in the Chukchi Sea achieved 50% size-at-maturity at 46 mm CW based on allometry of the abdominal flap or the presence of an egg clutch (Fig. 3.7B). Size-at-maturity could not be estimated for the Beaufort Sea because of low sample sizes.

3.4 Fecundity

A total of 306 mature females, ranging from 38 to 78 mm CW (Table 3.4, Fig. 3.8), were collected for fecundity estimates in the Chukchi Sea. Embryo production was directly related to body size in CW (linear regression, $r^2 = 0.50$, $p < 0.0001$, Fig. 3.8). Mean number of embryos per 1-mm bin CW ranged from 7,092 embryos (38 mm CW) to 49,164 embryos (78 mm CW) (Table 3.4).

4. Discussion

This study improves knowledge of standing stock and population structure of snow crabs in the Chukchi and Beaufort seas. Snow crabs occurred across the Chukchi shelf but were found only in a localized portion of the western Beaufort shelf and along the central Beaufort shelf break and upper slope. Our estimates of total biomass and sustainable yield of snow crabs in the Alaskan Arctic were considerably lower than previous estimates (NPFMC 2009), likely due to inclusion of more sampled stations that greatly increased coverage of the study regions and may have included areas with lower densities of snow crab. Both males and females in the Beaufort Sea reached larger sizes than conspecifics in the Chukchi Sea, even though there was considerable overlap in the size range of females between the seas. Despite size range differences, length-weight relationships were similar between the Chukchi and Beaufort seas for males, but not females. Our direct estimates of size-at-maturity for males and females in the Chukchi Sea found males mature at larger sizes than females.

4.1 Biomass, abundance, and sustainable yield

Estimated total snow crab biomass in this study was much lower in both the Chukchi and Beaufort seas compared with previous estimates from the Arctic FMP (see Table 3.2). The Arctic FMP also estimated Chukchi total snow crab biomass to be more than double that of the Beaufort Sea (66,491 mt and 29,731 mt, respectively; NPFMC 2009). The Arctic FMP used a total of 96 sampling stations in the Chukchi and 26 sampling stations in the Beaufort seas. The present study, in contrast, used 320 sampling stations in the Chukchi and 197 sampling stations in the Beaufort Sea, increasing the total survey area in the Chukchi Sea by 33% (145,200 km^2 versus 98,803 km^2) and in the Beaufort Sea by 90% (65,002 km^2 versus 6,280 km^2). This lower total (pristine) biomass, which were 50 and 95% lower than Arctic FMP estimates for the Chukchi and Beaufort seas, respectively, perpetuated into lower harvestable biomass estimates for the Beaufort Sea, although harvestable biomass in the Chukchi Sea remained zero since no male crabs larger than the marketable 100 mm CW were caught. Harvestable biomass in the Beaufort Sea (1,722 mt) was approximately 26% of the previously estimated 6,571 mt in the Arctic FMP and our estimate of maximum sustainable yield (97 mt) was about 79% lower than the Arctic FMP-calculated MSY of 453 mt (see Table 3.2). Our results underscore the need for precautionary management regarding commercial fishing activities in the Arctic Management Area. In this region, snow crab are an important prey species for marine mammal species and removal of snow crab biomass via a commercial fishery may have negative impacts on these species.

Although our results indicate much lower biomass, we estimated higher mean CPUE values for snow crabs in the Chukchi Sea (387,691 individuals km^{-2}) than a previous estimate that used Arctic Eis EBT trawl data only (212,000 individuals km^{-2}, Goddard et al. 2012). The

higher abundances we observed were due to the large numbers of very small (30 - 40 mm CW) crabs across the Chukchi Sea, which may indicate that large numbers of young juvenile crabs have recently settled in the area over the study period. There are many questions surrounding larval drift and settlement in the Chukchi Sea from adjacent areas (see *Fecundity* discussion below), but the presence of high abundances of juvenile crabs suggests that this region may be a nursery area for snow crabs after settlement. Abundance in the Beaufort Sea, including small crabs, was much lower than in the Chukchi Sea, with only 47 individuals km^{-2}. For comparison, a previous abundance estimate for the western Beaufort Sea found between 800 (unlined EBT) and 99,600 (lined EBT) individuals km^{-2}, depending on whether a net liner was used (Rand and Logerwell 2011). The use of a liner during that cruise presumably increased the number of small (< 30 mm CW) crabs that were retained in the trawl relative to unlined trawls, but the PSBT that was used in most cruises compiled in the present study also had a high selectivity for these small crabs. Thus we find it justified to assume that catches in our study represent the true abundances and are lower than previous estimates based on the inclusion of more locations with low crab abundances. The low numbers of total crabs recovered from the Beaufort Sea, compared with the adjacent Chukchi Sea, suggest that little local production occurs in that region and that crabs may migrate from adjacent areas to the Beaufort Sea near or after the terminal molt.

4.2 Size distributions and length-weight relationships

Snow crabs in the Chukchi Sea had a smaller maximum size (maximum size of 93 mm CW) than conspecifics in other geographic locations, except the adjacent north-central Bering Sea (90 mm CW, Kolts et al. 2015). The maximum size of 119 mm CW found in the Beaufort Sea (this study, also see Rand and Logerwell 2011) was more similar to the maximum size observed in the Gulf of St. Lawrence, Canadian Atlantic (120 mm CW, Sainte-Marie and Gilbert

1998) and 160 mm CW off the coast of western Greenland (Burmeister and Siegstad 2008). In the Pacific, maximum reported size in the Okhotsk Sea is 100 mm CW (Yanagimoto et al. 2004), and ~130 mm CW in the eastern Bering Sea (Turnock and Rugolo 2012). Thus, maximum size of snow crabs in the Beaufort Sea was similar to maximum sizes in these other regions (except for even larger crabs in Greenland). The consistently small crab sizes observed in the Chukchi Sea (and northern Bering Sea, Kolts et al. 2015) suggest that maximum size may be restricted in this region, which is puzzling. One possible reason for smaller maximum size at least in the northeastern part of the Chukchi Sea is the low bottom temperatures from persistent winter water that occurs on the shelf for a majority of the year (< -1°C, Weingartner et al. 2005). Similarly, it has been suggested that body size in adult crabs may be limited by the persistently cold bottom temperatures in the northern Bering Sea (Kolts et al. 2015). Temperature is a principal factor regulating size at terminal molt in snow crabs, and temperatures below 1°C can inhibit a positive energy balance in snow crabs reared in the lab (Foyle et al. 1989, Thompson and Hawryluk 1990). Low temperatures may also result in a higher frequency of skipped molting (Dawe et al. 2012), slowed growth, smaller growth increments per molt, and a shift to a biennial reproductive cycle (Kolts et al. 2015).

Cold bottom water temperatures (< 0 °C) also prevail on the Beaufort shelf, but a marked transition occurs at about 200 m depth, where warmer Atlantic water (up to ~0.5 °C) persists and extends to depths of 350 m (Crawford et al. 2012). In the Beaufort Sea, Logerwell et al. (2011) reported a strong association between snow crabs and cold waters (< -1.5 °C) on the upper Beaufort Sea slope; however, temperature measurements in that study were only shown to 140 m, which is above the warmer Atlantic layer where most crabs occur. A majority of the large female crabs and mature males collected in the Beaufort Sea during the present study were found

in waters around 0.5 °C around 200 m depth (Bluhm et al. 2015, Ravelo et al. 2015), possibly capitalizing on the warmer Atlantic water conditions where they are able to grow to sizes that are comparable to those of snow crabs in other regions with more moderate temperatures. This is consistent with observations of very large male crabs at greater depth (500-600 m) associated with soft substrates and warmer water temperatures along the Newfoundland slope, where they encounter a rich prey spectrum and energetically favorable temperature conditions to obtain large body sizes (Dawe and Colbourne 2002, Dawe et al. 2012). It also is possible that mature males migrate out of the shallow Chukchi and into deeper regions of the Beaufort Sea, similar to the ontogenetic size-related migrations they undertake in the Bering Sea (Orensanz et al. 2004, Ernst et al. 2005) and the Canadian Atlantic (Dawe and Colbourne 2002, Biron et al. 2008).

4.3 Size-at-maturity

Size-at-morphometric maturity for males in the Chukchi Sea was substantially larger with 62 mm CW in our study based on morphometrics compared with a previous estimate of 35 mm CW for Chukchi males based on presence of spermatophores (Paul et al. 1997). The smaller size-at-maturity based on spermatophore presence is explained by the fact that male snow crabs develop testes during their adolescence, before the terminal molt (Sainte-Marie et al. 1995). But, aside from differences in methodology for determining maturity state, this discrepancy in size-at-maturity in the Chukchi Sea may also be due to an actual increase in size-at-maturity in the region over the last 2-3 decades. As noted earlier, snow crab size-at-maturity is, among others, a function of temperature conditioning during early ontogeny (Orensanz et al. 2007, Sainte-Marie et al. 2008, Burmeister and Sainte-Marie 2010). Although fall and winter temperatures across the shelf are condensed to a narrow temperature range near-freezing (Woodgate et al. 2005), water temperatures show dramatic interannual differences and can span from below -1°C to ≥ 6 °C

(e.g., Day et al. 2013, Blanchard and Feder 2014). A generally increasing trend in the length of residence time of warmer waters across the Chukchi shelf (Shimada et al. 2006, Woodgate et al. 2005, 2006) may account for the observed increase in size-at-maturity in snow crabs on the Chukchi shelf, although maximum body sizes remain smaller than conspecifics in other regions.

Comparisons of size-at-maturity using allometric CH:CW ratios yields high variability across geographic locations. In the Gulf of St. Lawrence males are morphometrically mature at 40 mm CW (Sainte-Marie and Hazel 1992). Males in the southeastern Bering Sea and the Barents Sea achieve morphometric maturity at 100 mm CW (Turnock and Rugolo 2012, Dvoretsky and Dvoretsky 2011). Males in the north-central Bering Sea south of St. Lawrence Island and in the Chirikov Basin are morphometrically mature at 59 mm and 51 mm CW, respectively (Kolts et al. 2015), distinctly smaller than in our Chukchi Sea study area just to the north. Possibly, the persistent cold pool in the northern Bering Sea provides colder year-round temperatures than on most of the Chukchi Sea shelf (Wyllie-Echeverria and Wooster 1998), depressing male maximum size in the northern Bering Sea (Dawe et al. 2012).

We found more agreement with earlier studies in size-at-maturity for females in the Chukchi Sea. Females reached 50% size-at-maturity at 46 mm CW in the present study, identical to a previous estimate in the northeastern Chukchi Sea from over two decades ago (Paul et al. 1997), indicating size-at-maturity has been conserved in this region. Our estimate was also similar to reported size-at-maturity for females from the southeastern Bering Sea, Gulf of St. Lawrence, and Sea of Japan (50 mm CW for all regions; Ito 1967, Watson 1970, Jewett 1981, Orensanz et al. 2007). Several investigators suggest that female snow crabs tend to be smaller at maturity at the northern limit of their distribution due to reduced bottom temperatures at northern limits (Jewett 1981, Somerton 1981, Paul et al. 1997, Dawe et al. 2012, Kolts et al. 2015). Clinal

variation in size-at-maturity is well established in the eastern Bering Sea ranging from 55°N to 65°N (Zheng et al. 2001, Ernst et al. 2005, Orensanz et al. 2007) and in the Gulf of St. Lawrence, Canada (Sainte-Marie and Gilbert 1998), and further supported by the range of mature females collected in the northern Bering Sea (Kolts et al. 2015). In the northern Bering Sea, mature females ranged from 40 to 68 mm CW south of St. Lawrence Island and from 49 to 59 mm CW north of St. Lawrence Island in the Chirikov Basin (Kolts et al. 2015). Female size-at-maturity in the present study for the Chukchi Sea was slightly smaller (46 mm) compared with those the Bering Sea findings, contrary to this regional comparison for male crab size-at-maturity.

4.4 Fecundity

Estimates of fecundity (number of embryos per clutch) in our study were slightly lower compared with previous estimates for the Chukchi Sea (Jewett 1981) and with other regions. For example, a 55 mm CW Chukchi Sea female in our study would have a mean fecundity of 23,223 embryos. A 55 mm CW female in the southeastern Chukchi Sea was reported as carrying a mean of 28,600 embryos (Jewett 1981), and about 29,560 eggs in the northeastern Chukchi Sea (Paul et al. 1997). The same sized female in the Canadian Atlantic would carry about 24,470 embryos (Haynes et al. 1976), a southeastern Bering Sea female would have about 26,640 embryos (Jewett 1981), and a female in the north-central Bering Sea would have 24,390 embryos (see curves and equations for all areas in Fig. 11 of Kolts et al. 2015). A 55 mm CW female in the Sea of Japan is expected to carry a mean of 30,404 embryos (Kon and Sinoda 1992). Thus, while our fecundity estimates were lowest among these comparisons, embryo production for females in the Chukchi Sea seems to be around the same overall magnitude as in other regions. However, an important question that still remains is the survival rate of snow crab larvae during the pelagic stages and how much, if at all, females in the Chukchi Sea contribute to local production in the

Chukchi Sea. The presence of clutch-bearing females in the Chukchi Sea indicates that at least some local production occurs in the region, but the degree of dependence on larval supply from the Bering Sea is still unknown.

Larval advection has been postulated as an important source of crabs in the Chukchi and Beaufort seas (Clement et al. 2005, Hu and Wang 2010, Bluhm et al. 2015). This seems supported by the fact that genetically, snow crab in the Bering, Chukchi and Beaufort seas are considered a panmictic population, with strong gene flow among these regions (Hardy et al. 2011, Albrecht et al. 2014). Further, advection of zooplankton (incl. meroplankton) from the Bering Sea into the Chukchi Sea is well documented (e.g., Grebmeier et al. 2006, Hopcroft et al. 2008, 2010). The presence of mature females with egg clutches in the Chukchi Sea, however, warrants further investigation to evaluate the contributions of larval advection versus local production. In this context, it will be important in future studies to determine if females in the Chukchi Sea are on annual or biennial breeding cycles. This may be resolved by relating the stage of egg clutches to the state of ovaries (i.e., empty and spent in an annually breeding female versus plump and developing in a biennially breeding female, Orensanz et al. 2007). Annually breeding females will likely produce close to three times more eggs over their lifetime than a biannually breeding female, reducing the possible contribution of local reproduction if biennial breeding is prevalent, as has been found for the northern Bering Sea (Kolts et al. 2015) and as our field observations indicate (Bluhm and Iken, unpublished data). In addition, influx into the Chukchi Sea snow crab population may also not be limited to larval advection. The conspicuous lack of adult snow crabs in the range of 45-60 mm CW in the northern Bering Sea may suggest significant adult migration of these crabs into the southern Chukchi Sea, which could then contribute to local reproduction in the region (Kolts et al. 2015).

Summary and conclusions

Our results are intended to inform the management of the Alaskan Arctic snow crab stock and to expand our understanding of Arctic snow crab life history parameters and distribution trends in light of potential future fisheries or other, non-fishing activities. The lower total and harvestable biomass estimates presented here for the Chukchi and Beaufort seas compared with previous estimates from the Arctic FMP highlight the need to compile a large dataset that encompasses as much of the region of interest as possible and spans both high abundance and low abundance years. Biomass and abundance estimates presented here may be further improved with inclusion of molting probabilities (prevalence of skip-molting) and accurate size-at-age data, should those become available in the future. We found generally similar length-weight relationships in snow crabs between sexes and seas. Both size-at-maturity and fecundity estimates were within similar ranges as for snow crabs occurring in other geographic localities, albeit on the lower end. Our estimate of fecundity could be improved if information became available regarding the percentage of females on an annual versus biennial reproductive schedule.

Ultimately, the results of the present study support continued precautionary management and continuation of the moratorium on commercial harvest of Alaskan Arctic snow crab stocks. Specifically, there are many unknowns surrounding snow crab distribution and life history in these regions. Although we were able to re-estimate biomass and abundance, and provide new length-weight relationships, size-at-maturity, and fecundity data, we were unable to make reliable growth and natural mortality estimates. Knowledge of these key population parameters as estimated directly from the existing stock is necessary to improve population modeling. The presence of large male snow crabs in the Beaufort, but not the Chukchi Sea, continues to remain

puzzling, although we propose the likely role of temperature control as this has been proposed as a principal controlling mechanism for many life history processes of snow crab. Continued monitoring with the intent of augmenting the temporal coverage of snow crab size frequency distributions, biomass, and abundance, as well as investigations into the larval dispersal and migratory connectivity of snow crabs occurring in the Bering, Chukchi, and Beaufort regions, will greatly facilitate improved management of snow crabs as a potential future fishery resource.

Acknowledgements

We extend many thanks to the crews and all cruise participants of all cruises listed in Table 1, who were instrumental in sampling efforts during cruises. In particular, we are indebted to the many data providers including A. Blanchard (UAF), L. Cooper (UMCES), K. Dunton (UT Austin), J. Grebmeier (UMCES), S. Jewett (UAF), B. Konar (UAF), R. Lauth (NOAA), and L. Logerwell (NOAA). This study was made possible in part by samples collected in 2008 in the Beaufort Sea under funding provided by the US Department of the Interior's Mineral Management Service (MMS), Alaska Region (Interagency Agreement M07PG13152 and AKC-058) 2011 in the Beaufort Sea under BOEM Cooperative Agreement No. M10AC2004 "Beaufort Sea Marine Fish Monitoring in the Central Beaufort Sea" (BeauFish), U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), Alaska Outer Continental Shelf Region, Anchorage Alaska, as part of the BOEM Environmental Studies Program. Participation of KI and BB in the BeauFish field survey was supported by the Coastal Marine Institute (CMI, Award M11AC00003). Samples were also collected in the Beaufort Sea under the BOEM Agreement No. M12AC00011 "U.S.-Canada Transboundary Fish and Lower Trophic Communities Project" in 2012-2014. Samples in the Chukchi Sea were obtained with qualified

outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior under Agreement No. 10-CIAP-010 and under BOEM Cooperative Agreement No. M12AC00009 "Arctic Ecosystem Integrated Survey (Arctic Eis)". Some Chukchi Sea crab samples were also collected through the Russian-American Long-Term Census of the Arctic (RUSALCA) cruise and as such, this publication is the result in part of research sponsored by the Cooperative Institute for Alaska Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreements NA13OAR4320056 and NA08OAR4320870 with the University of Alaska. Snow crab data also were provided by the Arctic Marine Biodiversity Observing Network (AMBON) program in 2015, funded through the NOS Integrated Ocean Observations Systems with contributions from NOAA, BOEM and Shell Industry (award number NA14NOS0120158). Snow carb data provided during the 2014 and 2015 Arctic Nearshore Impact Monitoring in Development Area (ANIMIDA) program was funded through BOEM award number M13PCO0019.

References

Albrecht, G.T., Valentin, A.E., Hundertmark, K.J., Hardy, S.M. 2014. Panmixia in Alaskan populations of the snow crab *Chionoecetes opilio* (Malacostraca: Decapoda) in the Bering, Chukchi, and Beaufort Seas. J Crust Biol 34: 31-39.

Alunno-Bruscia, M., Sainte-Marie, B. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio* (Brachyura, Majidae), in the northwestern Gulf of St. Lawrence. Can J Fish Aquat Sci 55: 459-477.

Armstrong, D.A., Burgos, J., Ernst, B., Orensanz, J.M. 2008. Female effective reproductive output of the snow crab stock in the eastern Bering Sea. North Pac Res Board Final Rep Project 508. 165 pp.

Barber, W.E., Smith, R.L., Weingartner, T.J. 1994. Fisheries oceanography of the northeast Chukchi Sea. Final report to the Alaska Outer Continental Shelf Region of the Mineral Management Service, U.S. Department of the Interior, OCS Study MMS-93-0051. 101 pp.

Biron, M., Ferron, C., Moriyasu, M. 2008. Movement of adult male snow crab, *Chionoecetes opilio*, in the Southern Gulf of St. Lawrence and eastern Nova Scotia, Canada. Fish Res 91: 260-270.

Blanchard, A.L., Feder, H.M. 2014. Interactions of habitat complexity and environmental characteristics with microbenthic community structure at multiple spatial scales in the northeastern Chukchi Sea. Deep Sea Res II 102: 132-143.

Bluhm, B.A., Iken, K., Hardy, S.M., Sirenko, B.I., Holladay, B.A. 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7: 269-293.

Bluhm, B.A., Iken, K., Divine, L. 2015. Population assessment of snow crab, *Chionoecetes opilio,* in the Chukchi and Beaufort Seas, including oil and gas lease areas. Final Report OCS Study BOEM 2015-029, University of Alaska, Fairbanks, AK. 83 pp.

Britt, L.L., Lauth, R.R., Norcross, B.L. 2013. Draft report to Department of the Interior Bureau of Ocean Energy Management: Distribution of fish, crab and lower trophic communities in the Chukchi Sea AK-11-08. Interagency Agreement M12PG00018. University of Alaska, Fairbanks, AK. 52 pp.

Burmeister, A.D. 2002. Preliminary notes on the reproduction conditions of mature female snow crab (*Chionoecetes opilio*) from Disko Bay and Sisimiut, West Greenland *In* Crabs in cold water regions: biology management and economics *Edited by* A. J. Paul, E.G. Dawe, R. Elner, GS Jamieson, GH Kruse, RS Otto, B. Sainte-Marie, TC Shirley and D. Woodby. Alaska Sea Grant, Fairbanks, A.K. pp. 255-267.

Burmeister, A.D., Sainte-Marie, B. 2010. Pattern and causes of a temperature-dependent gradient of size at terminal moult in snow crab (*Chionoecetes opilio*) along West Greenland. Polar Biol 33: 775-788.

Burmeister, A.D., Siegstad, H. 2008. Assessment of snow crab in West Greenland 2008, Greenland Institute of Natural Resources, Nuuk. Vol 68.

Clement, J.L., Maslowski, W., Cooper, L.W., Grebmeier, J.M., Walczowski, W. 2005. Ocean circulation and exchanges through the northern Bering Sea: 1979-2001 model results. Deep-Sea Res II 52: 3509-3540.

Comeau, M., Conan, G.Y. 1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. Can J Fish Aquat Sci 49: 2460-2468.

Comeau, M., Conan, G.Y., Maynou, F., Robichaud, G., Therriault, J.C., Starr, M. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. Can J Fish Aquat Sci 55: 262-279.

Conan, G.Y., Comeau, M. 1986. Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. Can J Fish Aquat Sci 43: 1710-1719.

Crawford, R.E., Vagle, S., Carmack, E.C. 2012. Water mass and bathymetric characteristics of polar cod habitat along the continental shelf and slope of the Beaufort and Chukchi seas. Polar Biol 35: 179-190.

Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J Cons Int Explor Mer 33: 340-362.

Dawe, E.G., Colbourne, E.B. 2002. Distribution and demography of snow crab (*Chionoecetes opilio*) males on the Newfoundland and Labrador shelf. *In* Crabs in cold water regions: biology, management, and economics *Edited by* A.J. Paul, E.G. Dawe, R. Elner, G.S. Jamieson, G.H. Kruse, R.S. Otto, B. Sainte-Marie, T.C. Shirley, D. Woodby. University of Alaska Sea Grant, AK-SG-02-01, Fairbanks, AK, pp. 577-594.

Dawe, E.D., Mullowney, D. R., Moriyasu, M., Wade, E. 2012. Effects of temperature on size-at-terminal molt and molting frequency in snow crab *Chionoecetes opilio* from two Canadian Atlantic ecosystems. Mar Ecol Prog Ser 469: 279-296.

Day, R.H., Weingartner, T.J., Hopcroft, R.R., Aerts, L.A.M., Blanchard, A.L., Gall, A.E., Gallaway, B.J., Hannay, D.E., Holladay, B.A., Mathis, J.T., Norcross, B.L., Questel, J.M., Wisdom, S.S. 2013. The offshore northeastern Chukchi Sea, Alaska: A complex high-latitude ecosystem. Cont Shelf Res 67: 147-165.

Dvoretsky, A.G., Dvoretsky, V.G. 2011. Commercial fish and shellfish in the Barents Sea: Have introduced crab species affected the population trajectories of commercial fish? Rev Fish Biol Fisheries 25: 297-322.

Ernst, B., Orensanz, J.M., Armstrong, D.A. 2005. Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Can J Fish Aquat Sci 62: 250-268.

Ernst, B., Armstrong, D.A., Burgos, J., Orensanz, J.M. 2012. Life history schedule and periodic recruitment of female snow crabs (*Chionoecetes opilio*) in the eastern Bering Sea. Can J Fish Aquat Sci 69: 532-550.

Feder, H.M., Jewett, S.C., Blanchard, A. 2005. Southeastern Chukchi Sea (Alaska) benthos. Polar Biol 28: 402-421.

Foyle, T.P., O'Dor, R.K., Elner, R.W. 1989. Energetically defining the thermal limits of the snow crab. J Exp Biol 145: 371-393.

Frost, K.J., Lowry, L.F. 1983. Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea. *In* The Alaskan Beaufort Sea: Ecosystems and Environments. *Edited by* P.W. Barnes, D.M. Schell, and E. Reimnitz. Academic Press, Orlando, F.L. pp. 381-402.

Goddard, P., Lauth, R., Armistead, C. 2012. Results of the 2012 Chukchi Sea bottom trawl survey of bottomfishes, crabs, and other demersal macrofauna. US Dept Commer, NOAA Tech Memo NMFS-AFSC-278, 110 p.

Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B. 2006. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanog 71: 331-361.

Gross, J. 2015. Variability in the size frequency distribution and growth of snow crab (*Chionoecetes opilio*) and Arctic Lyre crab (*Hyas coarctatus*) in the Chukchi Sea from 2009 to 2013. Ph.D. dissertation, University of Fairbanks, Fairbanks, AK. 82 pp.

Gunderson, D.R., Ellis, I.E. 1986. Development of a plumb staff beam trawl for sampling demersal fauna. Fish Res 4: 35-41.

Hardy, S.M., Lindgren, M, Konacanchi, H, Huettmann, F. 2011. Predicting the distribution and ecological niche of unexploited snow crab (*Chionoecetes opilio*) populations in Alaskan waters: A first open-access ensemble model. Integr Compar Biol 51: 608-622.

Hartnoll, R.G. 1982. Growth. *In* The biology of the Crustacea. *Edited by* L.G. Abele. Academic Press, New York, N.Y. pp 111-196.

Haynes, E., Karinen, J.F., Watson, J., Hopson, D.J. 1976. Relation of number of eggs and egg length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering Sea and Gulf of St. Lawrence. J Fish Res Board Can 33: 2592-2959.

Hines, A.H. 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs. Mar Biol 69: 309-320.

Hopcroft, R.R., Bluhm, B.A., Gradinger, R. (eds). 2008. Arctic Ocean synthesis: Analysis of climate change impacts in the Chukchi and Beaufort Seas with strategies for future research. Fairbanks, AK. 184 pp.

Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A.I. 2010. Zooplankton community patterns in the Chukchi Sea during summer 2004. Deep Sea Res 57: 27-39.

Hu, H., Wang, J. 2010. Modeling effects of tidal and wave mixing on circulation and thermohaline structures in the Bering Sea. J Geophys Res 115: C01006, doi:10.1029/2008JC005175.

Ito, K. 1967. Ecological studies on the edible crab, *Chionoecetes opilio* (O. Fabricius), in the Japan Sea. I. When do female crabs first spawn and how do they advance into the following reproductive stage. Bull Jpn Sea Reg Fish Res Lab 17: 67-84.

Jewett, S.C. 1981. Variations in some reproductive aspects of female snow crabs *Chionoecetes opilio*. J Shellfish Res 1: 95-99.

Kolts, J.M., Lovvorn, J.R., North, C.A., Grebmeier, J.M., Cooper, L.W. 2013. Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea. Mar Ecol Prog Ser 483: 209-220.

Kolts, J.M., Lovvorn, J.R., North, C.A., Janout, M.A. 2015. Oceanographic and demographic mechanisms affecting population structure of snow crabs in the northern Bering Sea. Mar Ecol Prog Ser 518: 193-208.

Kon, T., Sinoda, M. 1992. Zuwai crab population. Mar Behav Physiol 21:185-226.

Logerwell, L., Rand, K. 2010. Beaufort Sea marine fish monitoring 2008: pilot survey and test of hypotheses. USDOI Alaska, OCS Region OCS Study MMS 2008-062.

Logerwell, L., Rand, K., Weingartner, T. 2011. Oceanographic characteristics of the habitat of benthic fish and invertebrates in the Beaufort Sea. Polar Biol 34: 1783-1796.

Moriyasu, M., Conan, G.Y., Mallet, P., Chiasson, Y., Lacroix, H. 1987. Growth per molt, molting season and mating of snow crab (*Chionoecetes opilio*) in relation to functional and morphometric maturity. ICES CM 1987/ K:21.

Moriyasu, M., Lanteigne, C. 1998. Embryo development and reproductive cycle in the snow crab *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. Can J Zool 76: 2040-2048.

Norcross BL, Holladay BA, Walker KL, Edenfield LE, (2015) Chapter 3.1. Length-weight-age relationships of demersal fishes on the shelf of the Alaskan Beaufort Sea, In: Central Beaufort Sea Marine Fish Monitoring, Final Rep, OCS Study, BOEM 2015-xxx

North Pacific Fishery Management Council (NPFMC). 2009. Fishery Management Plan for the Fish Resources of the Arctic Management Area. Anchorage, AK. 146 pp.

Orensanz, J.M., Ernst, B., Armstrong, D.A., Stabeno, P., Livingston, P. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an environmental ratchet? CalCOFI Rep 45: 65-79.

Orensanz, J.M., Ernst, B., Armstrong, D.A. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. J Crust Biol 27: 576-591.

Otto, R.S. 1998. Assessment of the eastern Bering Sea snow crab, *Chionoecetes opilio*, stock under the terminal molting hypothesis. *In* Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. *Edited by* G.S. Jamieson, A. Campbell. Can Spec Publ Fish Aquat Sci 125: 109-124.

Paul, J.M., Paul, A.J., and Barber, W.E. 1997. Reproductive biology and distribution of the snow crab from the northeastern Chukchi Sea. Am Fish Soc Symp 19: 287-294.

Rand, K.M., Logerwell, E.A. 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34: 475-488.

Ravelo, A.M., Konar, B., Trefry, J.H., Grebmeier, J.M. 2014. Epibenthic community variability in the northeastern Chukchi Sea. Deep-Sea Res II 102: 119-131.

Ravelo, A.M., Konar, B., Bluhm, B.A. 2015. Spatial variability of epibenthic communities on the Alaska Beaufort shelf. Polar Biol 38: 1783-1804.

Rugolo, L., Pengilly, D., MacIntosh, R., Gravel, K. 2005. Reproductive potential and life history of snow crabs in the eastern Bering Sea. *In* Bering Sea Snow Crab Fishery Restoration Research: Final Comprehensive Performance Report. NOAA, NMFS 99802-1668, Juneau, AK. pp 57-323.

Sainte-Marie, B., Hazel, F. 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of Saint Lawrence. Can J Fish Aquat Sci 49: 1282-1293.

Sainte-Marie, B., Raymond, S., Brethes, J. 1995. Growth and maturation of the male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Can J Fish Aquat Sci 52: 903-924.

Sainte-Marie, B., Gilbert, D. 1998. Possible effects of changes in CIL temperature and thickness on population dynamics of snow crab, *Chionoecetes opilio*, in the Gulf of Saint Lawrence. CSAS Research Document 98/38, 19 pp.

Sainte-Marie, B., Gosselin, T., Sévigny, J.M., Urbani, N. 2008. The snow crab mating system: opportunity for natural and unnatural selection in a changing environment. Bull Mar Sci 83: 131-161.

Shimada, K., Kamoshida, T., Itoh, M., Nishino, S., Carmack, E., McLaughlin, F., Zimmermann, S., Proshutinsky, A. 2006. Pacific Ocean inflow: Influence on catastrophic reduction of sea ice cover in the Arctic Ocean. Geophys Res Lett 33: L08605 http://dx.doi.org/10.1029/2005GL025624

Somerton, D.A. 1981. Regional variation in the size of maturity of two species of Tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Can J Fish Aquat Sci 38: 163-174.

Stearns, S.C. 1976. Life history tactics: a review of the ideas. Q Rev Biol 51:3-47.

Stichert, L. 2009. AK Depart Fish Game lab protocol: processing *Chionoecetes* crabs. Available from author, Kodiak. AK. 12 pp.

Thompson, R.J., Hawryluk, M. 1990. Physiological energetics of the snow crab, *Chionoecetes opilio*. *In* Proceedings of the International Symposium on King and Tanner Crabs. AK Sea Grant AK-SG-90-04:283-291.

Thompson, G.G. 1992. Management advice from a simple dynamic pool model. Fish Bull 90: 552-560.

Turnock, B.J., Rugolo, L.J. 2012. Stock assessment of eastern Bering Sea snow crab. North Pacific Fishery Management Council, PO Box 103136, Anchorage, AK. 116 pp.

Watson, J. 1970. Maturity, mating and egg-laying in the spider crab, *Chionoecetes opilio*. J Fish Res Board Can 29: 447-449.

Weingartner, T., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., Cavalieri, D. 2005. Circulation on the north central Chukchi Sea shelf. Deep-Sea Res II 52: 3150-3174.

Woodgate R.A., Aagaard, K., Weingartner, T.J. 2005. A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990-1991. Deep Sea Res II 52: 3116-3149.

Woodgate, R.A., Aagaard, K., Weingartner, T.J. 2006. Interannual changes in the Bering Strait fluxes of volume, heat and freshwater between 1991 and 2004. Geophys Res Lett 33: L15609 doi: 10.1029/2006GL026931

Wyllie-Echeverria, T., Wooster, W. S. 1998. Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish Oceanog 7: 159–170.

Yanagimoto, T., Yosho, I., Watanabe, K. 2004. Distribution and morphological maturation size of the snow crab, *Chionoecetes opilio* in the southwest area of the Okhotsk Sea in summer. Nippon Suisan Gakk 70: 750-757.

Zheng, J., Kruse, G.H. 2006. Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-down effects? Prog Oceanog 68: 184-204.

Zheng J, Kruse GH, Ackley DR. 2001. Spatial distribution and recruitment patterns of snow crabs in the eastern Bering Sea. *In* Spatial processes and management of marine populations. *Edited by* G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, D. Witherell. Alaska Sea Grant College Program AK-SG-01-02. Fairbanks, AK. pp 233-255.

Table 3.1. Cruise data showing the timing of sampling, project name, gear type used, and data provided for the current study. PSBT= plumb staff beam trawl, EBT= Nor'Eastern bottom trawl. Major funding sources indicated by superscripts.

Month/ Year	Project	Gear Type	Data Provided
Chukchi Sea			
Aug 2004	RUSALCA-1 [a]	PSBT	Biomass, abundance, size frequency
Aug 2007	Oscar Dyson [a]	PSBT	Biomass, abundance
Aug 2008	Oshoru Maru IPY [b]	PSBT	Biomass, abundance
Aug 2009	RUSALCA-2 [a]	PSBT	Biomass, abundance, size frequency, fecundity
Aug 2009	COMIDA [c]	PSBT	Biomass, abundance
Aug 2010	COMIDA [c]	PSBT	Biomass, abundance, size frequency, fecundity
Sept 2010	CSESP [d]	PSBT	Biomass, abundance, size frequency
Aug-Sept 2010	AKMAP [e]	PSBT	Biomass, abundance, size frequency
Sept 2011	AKMAP [e]	PSBT	Biomass, abundance, size frequency
Aug 2012	RUSALCA-3 [a]	PSBT	Biomass, abundance, size frequency, fecundity
Aug-Sept 2012	Arctic Eis [c]	PSBT, EBT	Biomass, abundance, size frequency, fecundity, size-at-maturity
Aug-Sept 2015	AMBON [a,c,d]	PSBT	Biomass, abundance, size frequency
Beaufort Sea			
Aug-Sept 2008	Western Beaufort Fish Survey [c]	EBT	Biomass, abundance
Aug-Sept 2011	BeauFish Survey [c,f]	PSBT	Biomass, abundance, size frequency
Sept 2012	Transboundary [c]	PSBT	Biomass, abundance, size frequency
Aug-Sept 2013	Transboundary [c]	PSBT	Biomass, abundance, size frequency
Aug-Sept 2014	Transboundary [c]	PSBT	Biomass, abundance, size frequency
Aug 2014	ANIMIDA [c]	PSBT	Biomass, abundance, size frequency
Aug 2015	ANIMIDA [c]	PSBT	Biomass, abundance, size frequency

Major funding sources: [a] NOAA: National Oceanographic and Atmospheric Administration; [b] Japanese Funding,
[c] BOEM: Bureau of Ocean Energy Management (in 2008 as Minerals Management Service), [d] Oil Industry (Shell Oil, Conoco Phillips, and/or Statoil), [e] DEC: Department of Environmental Conservation, [f] CMI: Coastal Marine Institute.

Table 3.2. Estimates of total and harvestable biomass in the Chukchi and Beaufort seas as determined in the Arctic FMP (NPFMC 2009) and based on the revised estimates (this study) for snow crabs. B_0 = pristine or unfished biomass, F_{MSY} = Fishing mortality at maximum sustainable yield (MSY), B_{MSY} = biomass at MSY, mt = metric tons.

Parameter	Arctic FMP	This study
Total B_0 (Chukchi Sea)	66,491mt	3,461 mt
Total B_0 (Beaufort Sea)	29,731mt	15,656 mt
Harvestable B (Chukchi Sea)	0 mt	0 mt
Harvestable B (Beaufort Sea)	6,571 mt	1,722 mt
F_{MSY}	0.36	0.36
B_{MSY}	1041 mt	272 mt
MSY	453 mt	97 mt
B_{MSY}/B_0	0.19	0.16
MSY/B_0	0.06	0.06

Table 3.3. Parameters used to establish selectivity for EBT and PSBT by minimizing the difference between the EBT and PSBT in the predicted proportions of snow crabs in each width bin. Parameter *a* is crab size (mm CW) at 50% selectivity, and parameter *b* is the steepness of the curve.

Parameters	EBT	PSBT
a	31.32	120.00
b	-0.32	0.57

Table 3.4. Mean number of eggs per clutch scaled to snow crab body size (carapace width, CW) and proportion of female snow crabs at each CW as determined from female size-at-maturity in the present study for the range of mature females observed in the Chukchi Sea (38 to 78 mm CW).

CW (mm)	mean # eggs per clutch	proportion mature
38	7,092	0.19
39	8,231	0.22
40	9,505	0.25
41	8,917	0.29
42	13,258	0.33
43	12,489	0.37
44	12,307	0.41
45	13,188	0.46
46	14,765	0.50
47	16,167	0.55
48	15,592	0.59
49	16,339	0.63
50	17,387	0.67
51	20,363	0.71
52	21,282	0.75
53	22,380	0.78
54	21,700	0.81
55	23,223	0.83
56	24,441	0.86
57	27,881	0.88
58	26,138	0.90
59	16,105	0.91
60	36,477	0.93
61	34,044	0.94
62	31,611	0.94
63	33,720	0.95
64	31,923	0.96
65	42,597	1.00
66	36,267	1.00
67	37,342	1.00
68	38,416	1.00
69	39,491	1.00
70	40,566	1.00
71	41,641	1.00
72	42,716	1.00
73	43,790	1.00
74	44,865	1.00
75	45,940	1.00
76	47,015	1.00
77	48,090	1.00
78	49,164	1.00

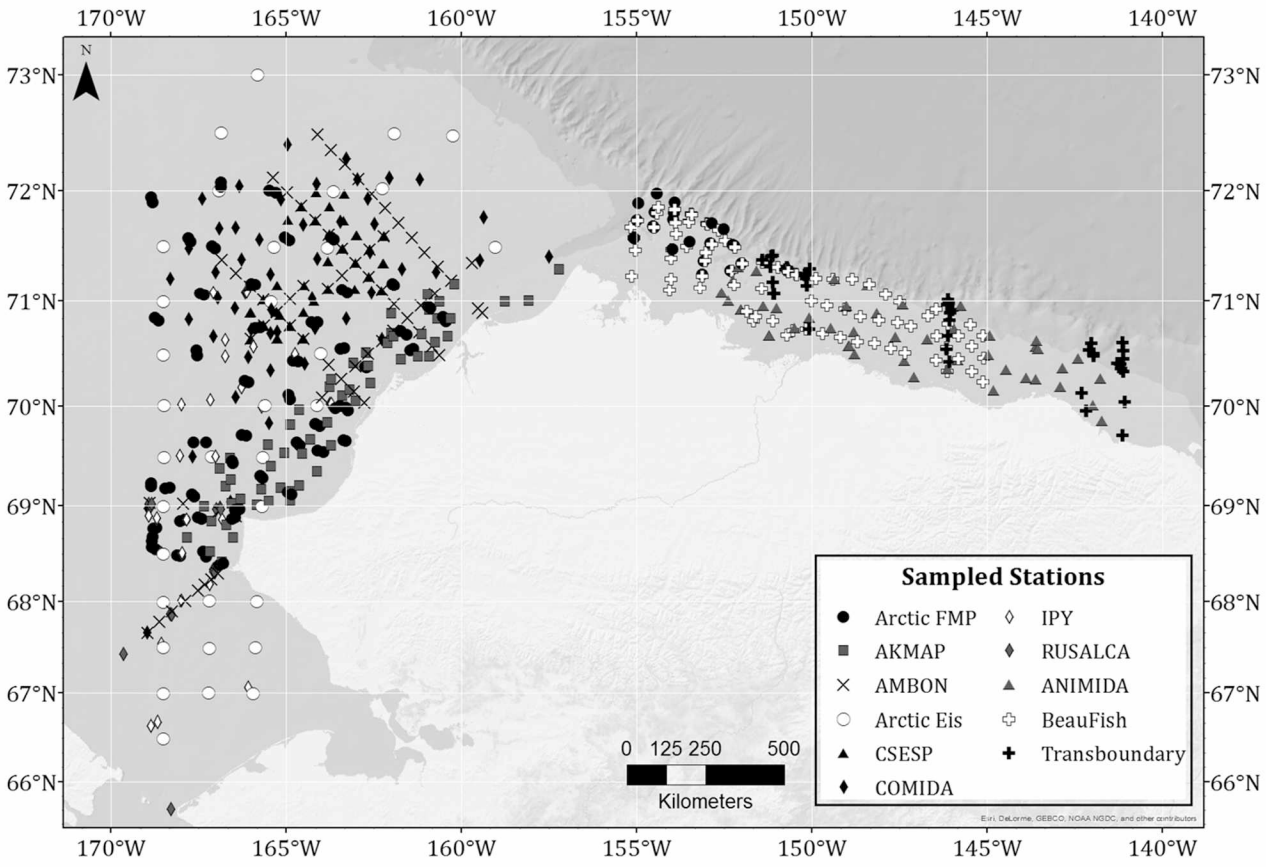

Figure 3.1. Stations sampled on the Alaska Chukchi and Beaufort Sea shelves from 2004 to 2015. Stations denoted as solid black circles in the Chukchi and Beaufort seas are stations that contributed to biomass estimates in the Arctic FMP (Barber et al. 1994, NPFMC 2009, Rand and Logerwell 2011). White gridded lines at 1°latitude and 1°longitude are provided as reference for station groupings that were pooled at this level for the Chukchi region to account for temporal and spatial variability in area coverage.

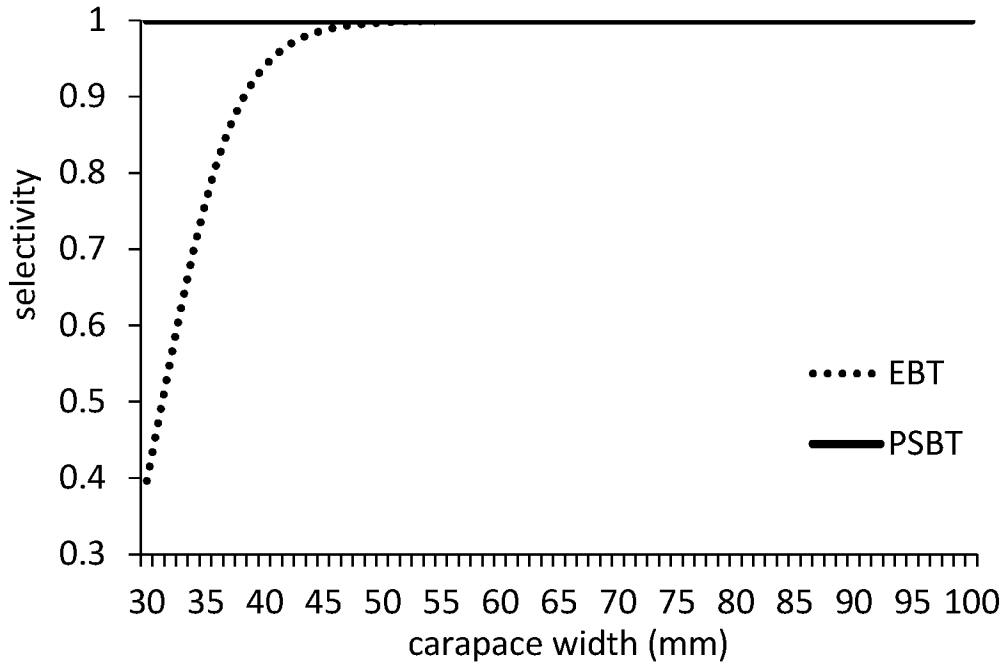

Figure 3.2. Selectivity for two gear types: the Nor'Eastern Bottom Trawl (EBT) and the Plumb Staff Beam Trawl (PSBT) during the Arctic Eis 2012 bottom trawl cruise for the range of snow crab carapace widths captured.

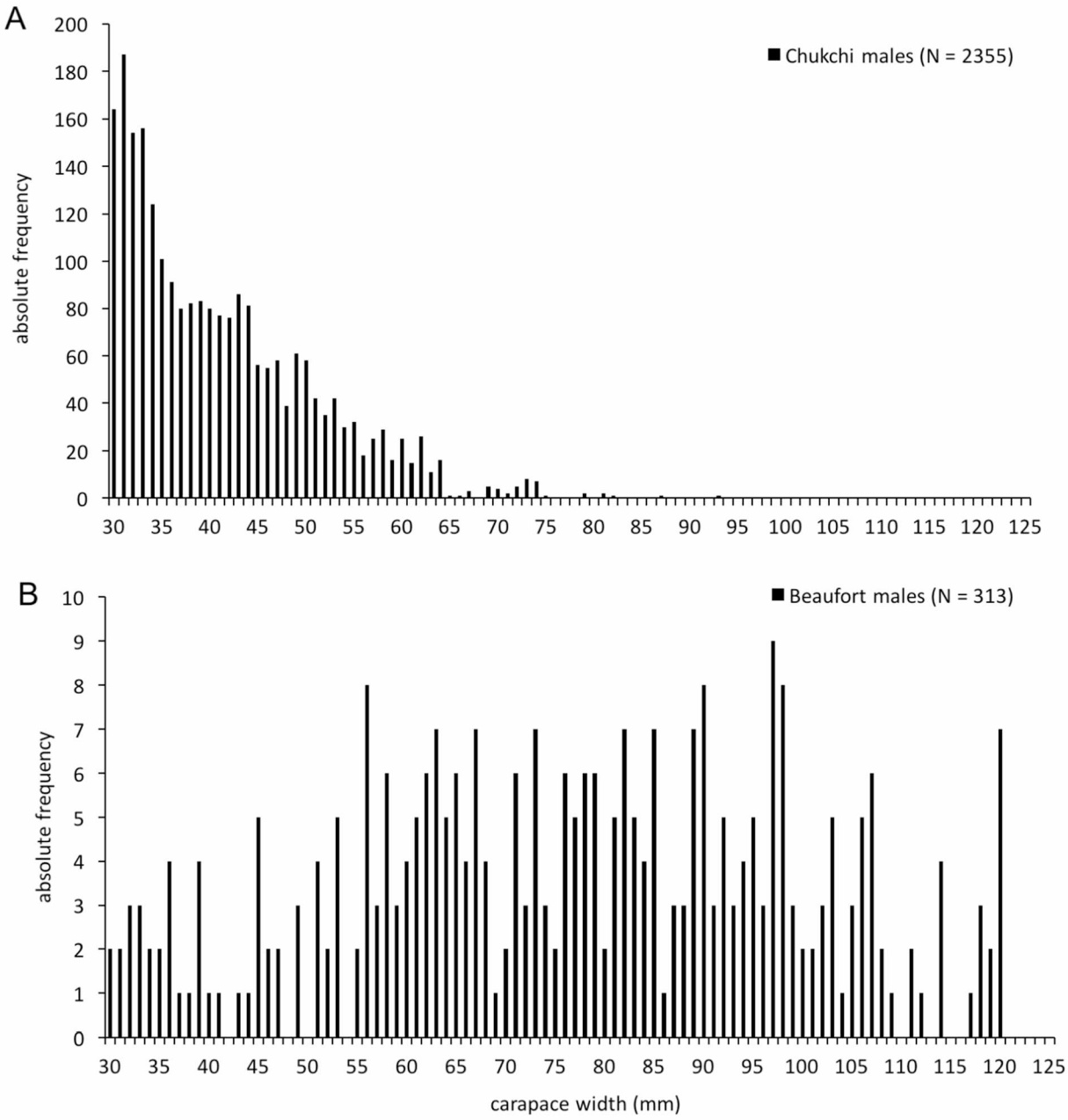

Figure 3.3. Size frequency distributions for males ≥ 30 mm CW in the A) Chukchi collected from 2004 to 2015 and B) Beaufort Seas collected from 2008 to 2015. Note the different scales of the y-axes.

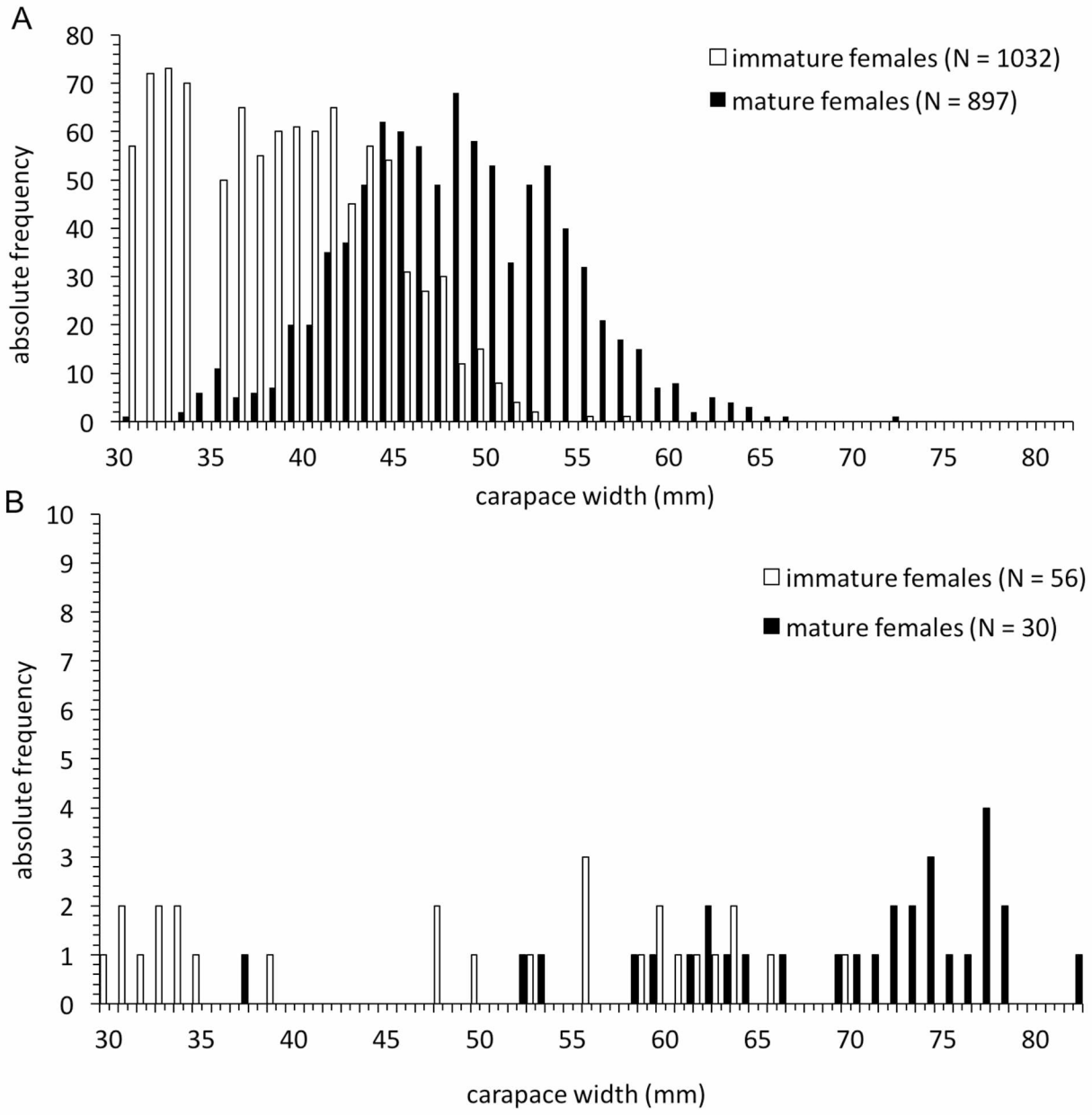

Figure 3.4. Size frequency distributions for immature and mature females ≥ 30 mm CW (A) in the Chukchi Sea collected from 2004 to 2015, and (B) immature and mature females collected in the Beaufort Sea from 2008 to 2015. Note the different scales of the y-axes.

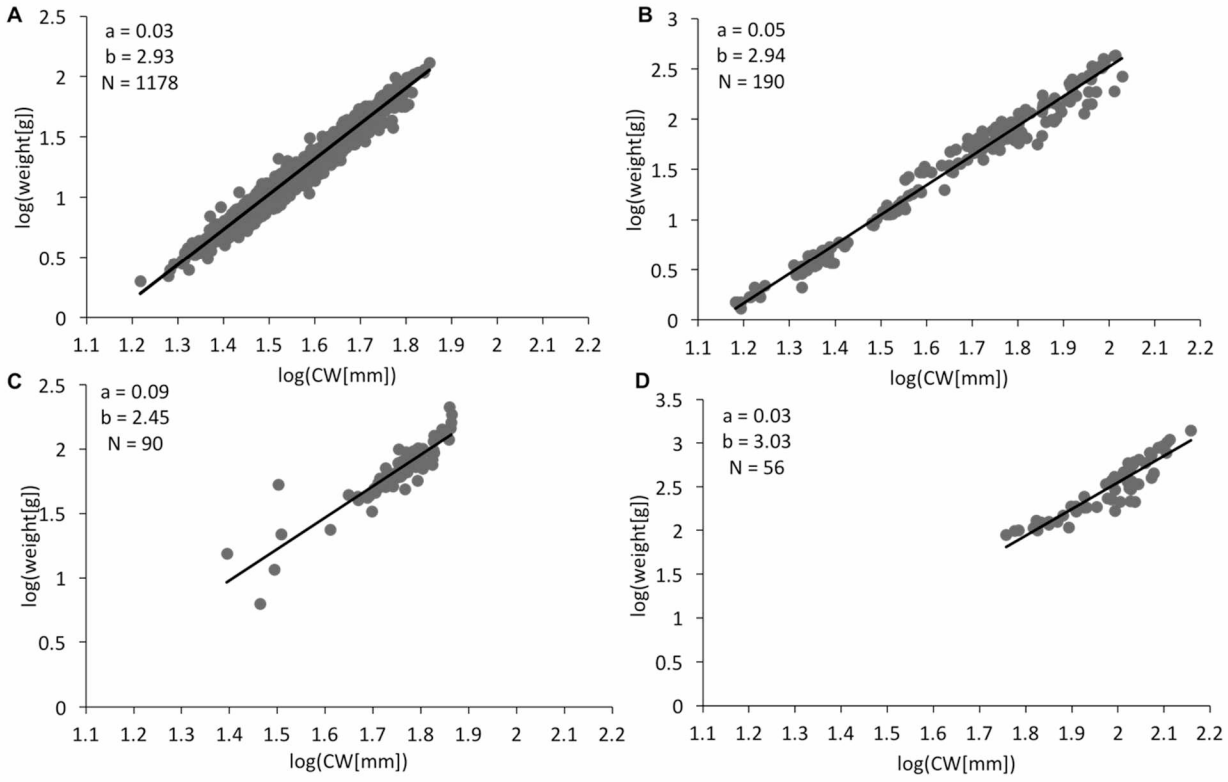

Figure 3.5. Linear regressions showing the log-transformed length-weight relationships of A) Chukchi Sea immature males, B) Beaufort Sea immature males, C) Chukchi Sea mature males, D) Beaufort Sea mature males estimated from male snow crabs collected from 2004 to 2015. Parameters (*a* and *b*) and sample sizes (N) are presented in the respective figures.

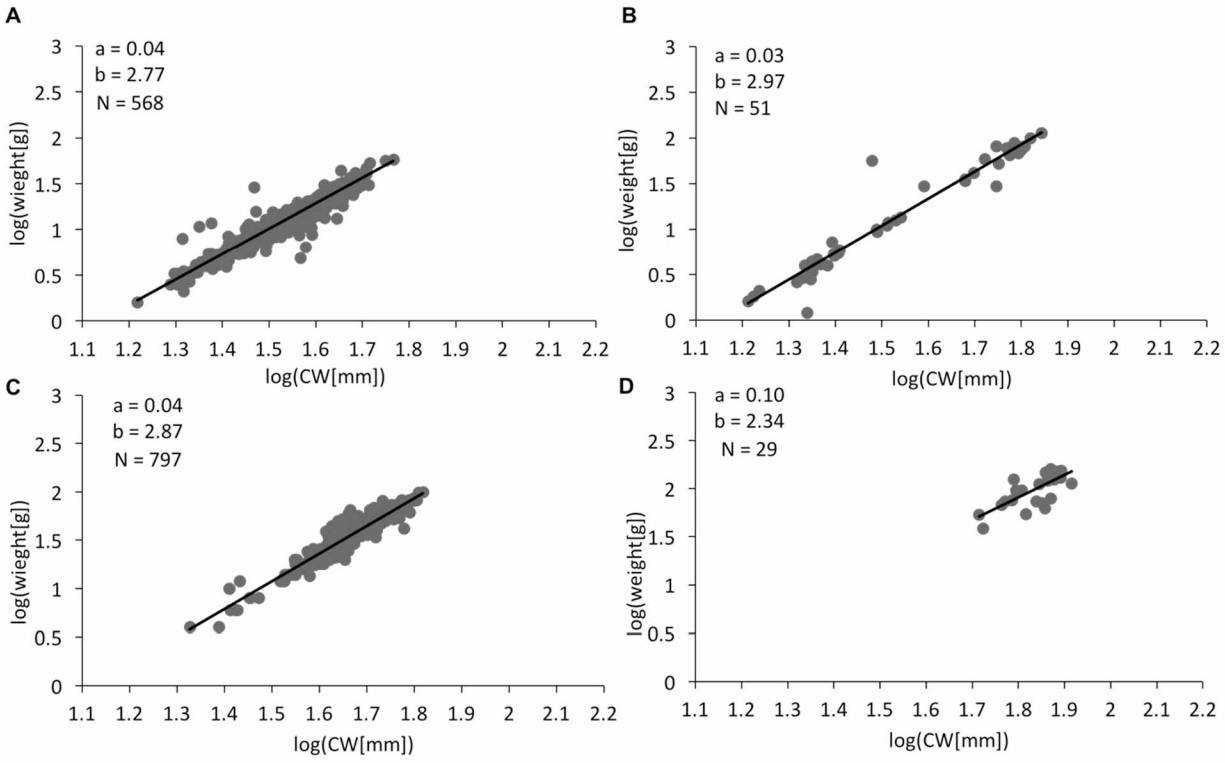

Figure 3.6. Linear regressions showing the log-transformed length-weight relationships of A) Chukchi Sea immature females, B) Beaufort Sea immature females, C) Chukchi Sea mature females, D) Beaufort Sea mature females estimated from female snow crabs collected from 2004 to 2015. Parameters (*a* and *b*) and sample sizes (N) are presented in the respective figures.

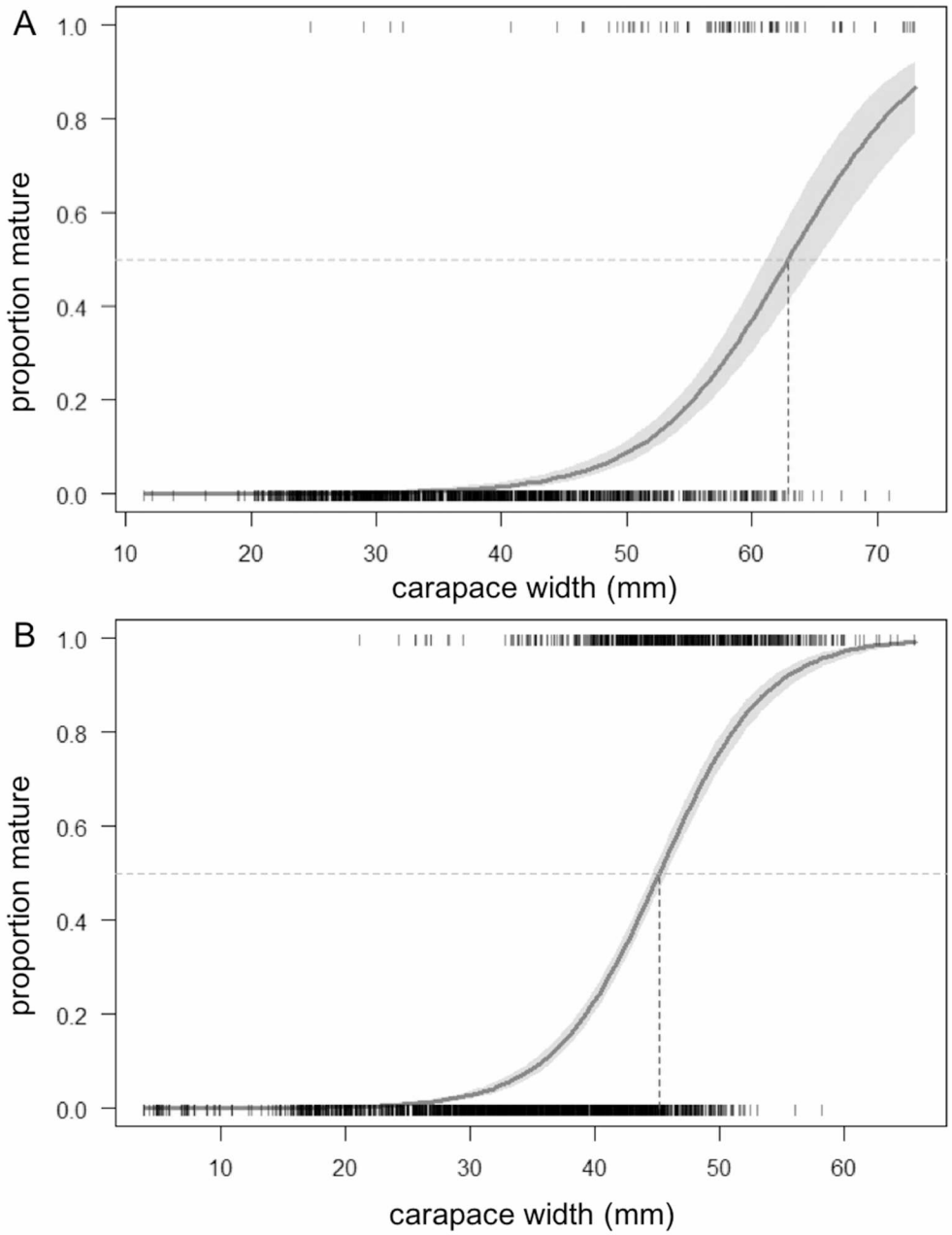

Figure 3.7. Size-at-maturity (dark gray solid lines) with 95% confidence intervals (light gray shaded areas) for (A) males and (B) females estimated from snow crabs collected in the Chukchi Sea. Size at which 50% of all crabs are mature is denoted at the intersection of the gray dashed lines. Short black lines at top and bottom of graphs indicates individual snow crabs that are either mature (top lines) or immature (bottom lines).

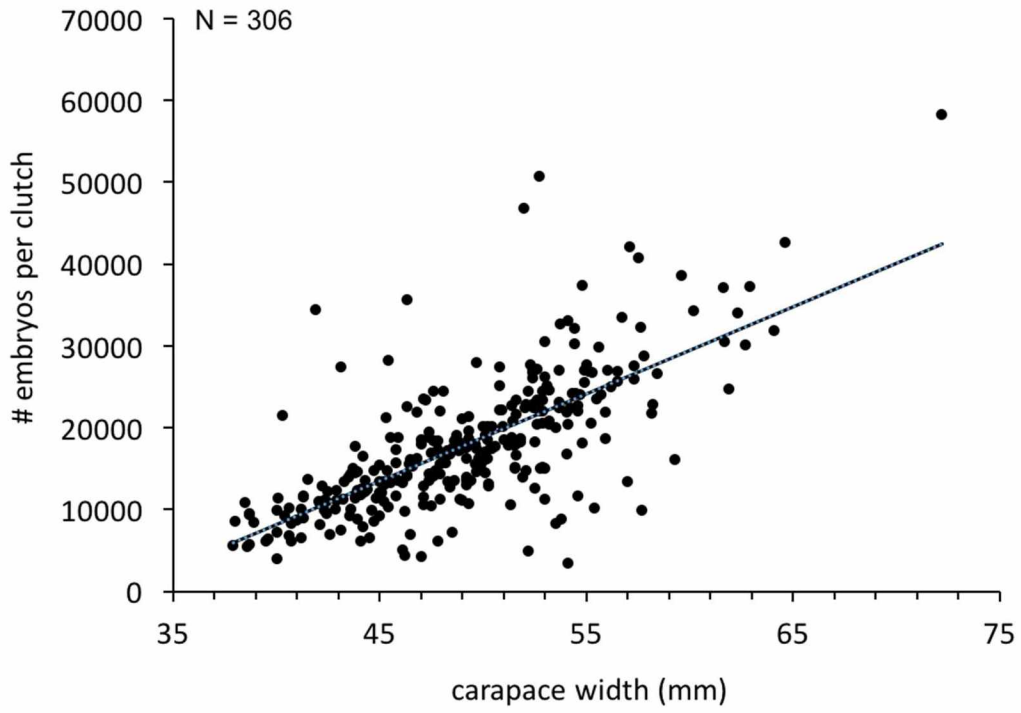

Figure 3.8. Fecundity as number of embryos plotted against body size (carapace width) per mature female snow crab collected from the Chukchi Sea from 2009 to 2012. Number of embryos in a clutch= 1,063.7 · CW – 34,379, r^2= 0.50 (linear regression fit), $p < 0.0001$.

CONCLUSIONS

This study contributed important ecological baseline knowledge regarding snow crab position in Alaskan Arctic benthic food webs and its specific dietary requirements, as well as expanding on snow crab life-history and population dynamics in the Chukchi and Beaufort seas. The Chukchi and Beaufort seas are experiencing dramatic climatic changes (e.g. Barber et al. 2015); as a biomass-dominant epibenthic omnivore in these regions (Bluhm et al. 2009, Rand and Logerwell 2011, Ravelo et al. 2014, 2015), snow crab will no doubt be impacted by ongoing and future changes to Alaskan Arctic benthic ecosystems. Specifically, changes in sea ice timing extent, and duration may shift future production regimes in the Chukchi Sea from a benthic dominated system to one dominated by pelagic food webs (Arrigo et al. 2008, Grebmeier 2012). Although currently a minor part of the energy is channeled through pelagic food webs in the Chukchi Sea (Whitehouse et al. 2014), environmental changes such as increased water volume transport through the Bering Strait and earlier ice retreat (Woodgate et al. 2006, 2010), which favor increased zooplankton abundance, may greatly reduce the amount of carbon exported to the benthos (Carroll and Carroll 2003, Grebmeier 2012). Reduced vertical carbon export provides overall less energy to fuel benthic production and could impact the snow crab prey field via altered benthic community composition, size frequency distributions of benthic invertebrates, and may increase predation pressure on snow crabs via increased predator abundances (Hardy et al. 2011, Grebmeier 2012, Grebmeier et al. 2015). The information provided by this study regarding the trophic role and dietary requirements of snow crabs in the Alaskan Arctic improves our ability to predict how future changes or disturbances to benthic environments may impact this species.

My first chapter provided the first detailed information regarding the trophic structure and vulnerability of regional benthic food webs on the Alaska Beaufort shelf of which snow crabs are a member. Differences in trophic structure among nearshore eastern and central Beaufort Sea regions are related to proximity to freshwater sources delivering terrestrial input into the marine environment (Divine et al. 2015a). Terrestrial carbon is reflected in stable $\delta^{13}C$ and $\delta^{15}N$ isotope analysis of consumer tissues, reflective of long-term exposure to terrestrial carbon. Across the western shallow and deep (along the shelf break and upper slope 180 to 220 m depth) Beaufort shelf, benthic food webs exhibit intermediate trophic redundancy (i.e., the degree of dietary overlap among taxa within a food web in $\delta^{13}C$–$\delta^{15}N$ space) with consumers occupying intermediate trophic levels indicative of overlapping diets and shared trophic niche space among consumers, including snow crabs as predator/scavengers. In the central deep Beaufort region, however, there is little trophic redundancy and large trophic niche separation among consumers relative to other regions, due to the few taxa that are spread among a wider range of trophic levels. Low trophic redundancy and high niche separation among benthic invertebrate consumers of the central Beaufort food web suggest that this region in particular is more vulnerable to the effects of climate change such as changes in productivity, ocean temperatures, and sea ice dynamics. Snow crabs are a benthic predator/scavenger in western shallow and deep (system with trophic redundancy) and central deep Beaufort (low trophic redundancy) food webs, with most large males (i.e., > 100 mm carapace width) occurring in the central deep Beaufort. A disturbance in the energy flow through the low resiliency benthic food web in this latter region, for example the loss of taxa from fisheries biomass removal or oil and gas activity, may have more intense cascading effects on the intermediate and upper trophic level

benthic predators including snow crabs, in the central deep Beaufort than in other regions of the Beaufort Sea (Worm and Duffy 2003, Layman et al. 2007, Divine et al. 2015a).

I found that diets of snow crab differ between the Chukchi and Beaufort seas, which in part has been explained by spatial variability in benthic prey communities and by the size ranges and sex classes of snow crabs occurring in these regions (Divine et al. 2015b). Within the Chukchi Sea, snow crabs have similar diets between southern and northern regions and feed proportional to the most abundant prey taxa in those regions. I also observed moderate amounts of cannibalism from stomach content analysis in the Chukchi Sea. Cannibalism has been suggested as a contributing factor in controlling recruitment in snow crab stocks (Lovrich and Sainte-Marie 1997), and the high abundances of crabs on the Chukchi shelf may induce density-dependent cannibalism of early benthic instars and subsequently exert some control on year-class strength in the Chukchi Sea. Cannibalism was not apparent in the Beaufort Sea, and this was expected since generally low abundances of snow crabs occurred throughout the study period, indicating densities, especially of small instar individuals, might occur below levels that induce cannibalistic interactions among conspecifics (Lovrich and Sainte-Marie 1997). Predator size drives the upper and lower thresholds of vulnerability to cannibalism, thus at overall low densities small crabs are less likely to be cannibalized (Lovrich and Sainte-Marie 1997).

In combination, both snow crab diets (chapter 2) and trophic role in the central Beaufort Sea (chapter 1) are distinct from the Chukchi and western Beaufort areas. Again, snow crabs in the central Beaufort Sea are part of the unique benthic food web that is comprised of lower trophic redundancy and high trophic niche separation relative to the western Beaufort and the Chukchi Sea (Divine et al. 2015a). Snow crabs in the central Beaufort regions have a fairly specific diet and consumed primarily one species of polychaete, with some additional

consumption of ophiuroids, bivalves, and amphipods. Snow crabs in this system could be vulnerable to prey species range expansions and invasions and/or changes to community composition, which have already been recorded in the Pacific Arctic and sub-Arctic (Grebmeier 2012). This could be exacerbated with possible additional pressures in the future, such as a potential fishery of snow crabs in the Arctic.

Beyond improving our understanding of the trophic ecological roles of snow crabs in the Chukchi and Beaufort seas, the results of my dissertation provide important and updated information regarding Alaskan Arctic snow crabs as a potential future fishery resource (chapter 3). Snow crabs are the only invertebrate species identified as a potential target fisheries species by the Arctic Fishery Management Plan (Arctic FMP, NPFMC 2009). One shortcoming of the fisheries estimates of snow crab in the Arctic FMP and in the present study is the use of population parameters that were borrowed from other stocks or were assumed (NPFMC 2009). The present study offers improved estimates by providing direct measures for size-at-maturity, fecundity and by including considerably more snow crab distribution data (chapter 3). The new biomass and abundance data provided here suggest that snow crab biomass in the Chukchi Sea is comprised of high numbers of small (i.e., sub-marketable) crabs, whereas the Beaufort Sea supports some commercial-sized snow crabs, but in very low abundances. With regards to future potential fishing activities, it is important to note where snow crabs are most concentrated as fishing activities would be focused in those regions.

Depending on the type of fishery executed (i.e., pot fishery versus trawl fishery), impacts to overall benthic communities may be especially important to consider. As known from other Arctic regions of the world (McConnaughey and Syrjala 2014, Buhl-Mortensen et al. 2016), a fishery repeatedly utilizing bottom trawl gear to catch snow crabs may have detrimental impacts

on the benthos and trigger restructuring of benthic communities in a manner that may be unfavorable or unable to support large crabs in the future. For example, I identified the central Beaufort benthic food web as potentially vulnerable to future changes or disturbances (Divine et al. 2015 a, b). Because the only large male crabs observed during this study occurred on the western and central Beaufort shelf and upper slope, fishing would most likely occur in these regions (chapter 3), yet such fishing activities may impact benthic communities in such a manner that reduces the ability of snow crab to persist and support a sustainable fishery over time.

Ultimately, the results of the present study present a new milestone in our understanding of Arctic snow crab biology and potential fishery but also highlight the need for continued precautionary management of the currently unfished Alaskan Arctic snow crab stocks. Many unknowns, such as timing, duration, and types of gear allowed, still surround how a commercial fishery would be executed in the Beaufort Sea where large males suitable for a fishery occur. Additionally, time-series coverage of snow crab size frequency distributions, biomass, and abundance, as well as identification of annual versus biannual breeding and prevalence of skip-molting, are needed to supplement the aspects of population dynamics addressed in the present study. Increased knowledge of larval dispersal and connectivity among the Bering, Chukchi, and Beaufort seas would also provide valuable life history information regarding Alaskan Arctic snow crab. Snow crabs are an ecologically and commercially important species, thus continued monitoring will greatly facilitate improved management of this resource.

References

Arrigo KR, van Dijken G, Pabi S (2008) Impact of a shrinking Arctic ice cover on marine primary production. Geophys Res Lett 35:L19603 doi:10.1029/2008GL03502

Barber, DG, Hop, H, Mundy, CJ, Else, B, Dmitrenko, IA, Tremblay, JE, Ehn, JK, Assmy, P, Daase, M., Candlish, L.M., Rysgaard, S. 2015. Selected physical, biological and biogeochemical implications of a rapidly changing Arctic marginal ice zone. Prog Oceanog 139: 122-150.

Bluhm BA, Iken K, Hardy SM, Sirenko BI, Holladay BA (2009) Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7:269-293

Buhl-Mortensen L, Ellingsen KE, Buhl-Mortensen P, Skaar KL, Gonzalez-Mirelis G (2016) Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on density, diversity, and composition. ICES J Mar Sci 73:S98-i114

Carroll, ML, Carroll, J. 2003. The Arctic seas. *In* Biogeochemistry of marine systems *Edited by* K.D. Black, G.B. Shimmield. Blackwell Publishing, Oban, UK. pp 127-156.

Divine LM, Iken K, Bluhm BA (2015a) Regional benthic food web structure on the Alaska Beaufort Sea shelf. Mar Ecol Prog Ser 531:15-32

Divine LM, Iken, K, Bluhm BA (2015b) Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Deep-Sea Res II, doi: http://dx.doi.org/10.1016/j.dsr2.2015.11.009

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Ann Rev Mar Sci 4:63-78

Grebmeier JM, Bluhm BA, Cooper LW, Danielson S, Arrigo K, Blanchard AL, Clark JT, Day RH, Frey KE, Gradinger RR, Kędra M, Konar B, Kuletz KJ, Lee SH, Lovvorn JR,

Norcross BL, Okkonen SR (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanog 136:92-114

Hardy SM, Lindgren M, Konakanchi H, Huettmann F (2011) Predicting the distribution and ecological niche of unexploited snow crab (*Chionoecetes opilio*) populations in Alaskan waters: a first open-access ensemble model. Integr Comp Biol 51:608-622

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42-48

Lovrich GA, Sainte-Marie B (1997) Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura; Majidae), and its potential importance to recruitment. J Exp Mar Biol Ecol 211:225-245

McConnaughey RA, Syrjala SE (2014) Short-term effects of bottom trawling and a storm event on soft-bottom benthos in the eastern Bering Sea. ICES J Mar Sci 71:2469-2483

North Pacific Fishery Management Council (NPFMC). 2009. Fishery Management Plan for Fish Resources of the Arctic Management Area. Anchorage, AK. 146 pp.

Rand KM, Logerwell EA. 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475-488

Ravelo AM, Konar B, Trefry JH, Grebmeier JM. 2014. Epibenthic community variability in the northeastern Chukchi Sea. Deep-Sea Res II 102:119-131

Ravelo AM, Konar B, Bluhm BA. 2015. Spatial variability of epibenthic communities on the Alaska Beaufort shelf. Polar Biol 38:1783-1894

Whitehouse, GA, Aydin, K, Essington, TE, Hunt, GL 2014. A trophic mass balance model of the eastern Chukchi Sea with comparisons to other high-latitude systems. Polar Biol 37:911-

939

Woodgate RA, Aagaard K, Weingartner TJ (2006) Interannual changes in the Bering Strait fluxes of volume, heat and freshwater between 1991 and 2004. Geophys Res Lett 33:L15609

Woodgate RA, Weingartner TJ, Lindsay R (2010) The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. Geophys Res Lett 37:L01602

Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. Trends Ecol Evol 18:628-632